THE POPULATION ECOLOGY OF RED-BILLED GULLS

(*LARUS NOVAEHOLLANDIAE SCOPULINUS*) OF KNOWN AGE

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Doctor of Philosophy in Zoology
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by

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1. INTRODUCTION

The Red-billed Gull *Larus novaehollandiae scopulinus* is endemic to New Zealand and is one of the commonest gulls on the coast. There have been no detailed studies of this gull other than some work on food (Gurr, 1947), breeding distribution (Gurr & Kinsky, 1965; Mills, 1969), and general accounts in Stead (1932) and Oliver (1955). There is, however, knowledge of the seasonal dispersal (Carrick, Wheeler & Murray, 1957), population regulation (Carrick & Murray, 1964), general breeding biology (Wheeler & Watson, 1963), and seasonal mortality (v. Tets, 1968) of the closely related Silver Gull *L. n. novaehollandiae* in south-eastern Australia.

The present study has been confined to the population of gulls hatched or breeding at the Kaikoura Peninsula. This population is particularly suitable for research since annual banding of nestlings from 1958-59 has resulted in birds of known age forming a large proportion of the population. This banded population has provided not only the opportunity to study the influence of age on the breeding biology, but also the chance to follow the progress of individual known-aged birds. This has allowed aspects such as mortality and pair bond retention or change of mate and their effects on the breeding biology to be studied.

The major contributions to knowledge of the influence of age on the breeding biology and population dynamics of sea birds have been made by Austin (1945) on the Common Tern *Sterna hirundo*, Richdale (1949, 1957) on the Yellow-eyed Penguin *Megadyptes antipodes*, Coulson & White (1958, 1960) and Coulson (1966) on the Kittiwake Gull *Rissa tridactyla*, and Potts (1969) on the Shag *Phalacrocorax aristotelis*. It is hoped that the present study will make a further contribution to this subject.

Studies at the Kaikoura colonies began in 1964 as partial fulfilment for an M.Sc. degree. Quantitative data on clutch size and breeding success with special reference to the effect of age have already been described (Mills, 1967), from information collected in the 1964-65 and 1965-66 breeding seasons. The present study describes the results obtained to October 1969 and incorporates some of the data collected in the first two seasons.

The initial part of this thesis is devoted to a general description of the breeding cycle. Later sections examine the factors affecting the breeding biology with special reference to the clutch size and chick survival, the population loss from emigration and mortality and the recruitment to the population from immigration.

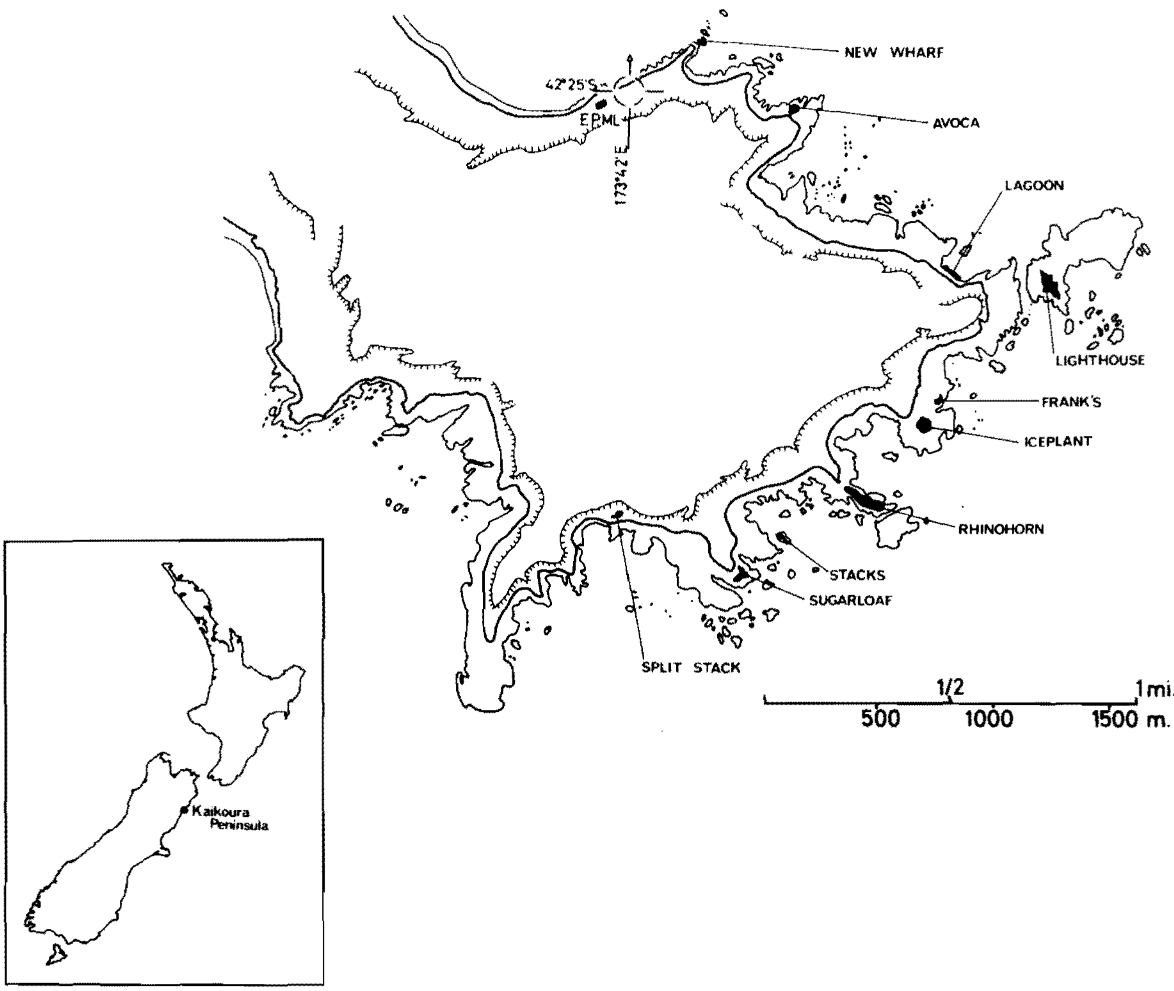

NEW WHARF
42°25'S
EPML
173°42'E
AVOCA
LAGOON
LIGHTHOUSE
FRANK'S
ICEPLANT
RHINOHORN
STACKS
SUGARLOAF
SPLIT STACK
1/2
1 mi.
500
1000
1500 m.
Kaikoura Peninsula

FIGURE 1. Map of Kaikoura Peninsula with the location of the Red-billed Gull colonies.

2. STUDY AREA AND HISTORY OF THE KAIKOURA POPULATION

The breeding colonies at Kaikoura are located on headlands of the north-eastern and south-eastern coasts of the peninsula (Figure 1). With the exceptions of the Lagoon Colony and a portion of the Sugarloaf Colony, all colonies are isolated from the mainland at low tides.

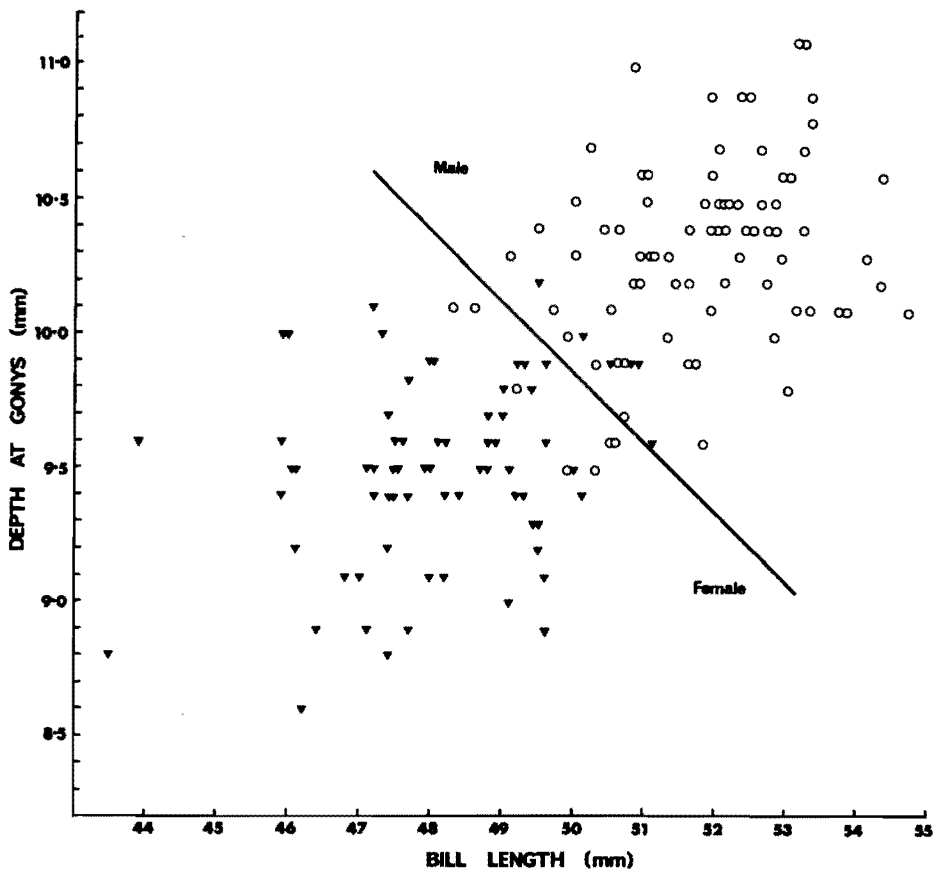
The Kaikoura colonies are the largest in the South Island and the third largest in New Zealand. They are undoubtedly ancient gulleries. The first reference to them is in a Maori legend which tells how an early explorer, Rakaihouia, was forced to stop at Kaikoura to feast on gulls' eggs because his provisions were low (Sherrard, 1966).

Although no accurate counts are available prior to 1964-65, visits since 1950 have indicated a steady increase in numbers. In 1953-54 breeding was confined to two headlands (B.D. Bell, pers. comm.). By 1964-65 breeding occurred on six colonies, the largest being the two original nesting sites (Lighthouse and Rhinohorns colonies). Between 1964-65 and 1968-69 a further three colonies were established. Details of counts made since 1964 are given in Table 1.

The population increase apparently began after 1932. Before then, the Red-billed Gull was rarely seen except on Banks Peninsula (Stead, 1932), but since then the number of Red-billed Gulls has increased and large populations are now found on the Canterbury coast and inland at Christchurch and Kaiapoi. The evident population increase in the Canterbury district is representative of the increase that has taken place throughout New Zealand. A similar trend of population increase has occurred in many sea bird species in the last twenty years.

TABLE 1. Number of pairs of Red-billed Gulls breeding at Kaikoura Colonies

Colony	1964-65 (22 Dec.)	1965-66 (28 Nov.)	1968-69 (5 Dec.)
Lighthouse	1565	1642	1882
Rhinohorns	1309	1317	1770
Iceplant	504	900	922
Sugarloaf	552	413	109
Stacks	c150	c150	451
Split Stack	c100	c100	c150
New Wharf	c200	c200	c100
Avoca		30	45
Frank's			129
Lagoon			120



DEPTH AT GONYS (mm)
11·0
10·5
10·0
9·5
9·0
8·5
Male
Female
44
45
46
47
48
49
50
51
52
53
54
55
BILL LENGTH (mm)

FIGURE 2. The relation between depth at gonys and bill length in 88 male and 77 female Red-billed Gulls from the Kaikoura population. The line which separates males and females is derived from the discriminant function analysis; [Depth at Gonys + (0.26102 x Length of Bill)]. The point of discrimination is 22.875, males above, females below this value.

3. METHODS OF STUDY

The gulls have been studied at the Kaikoura colonies for part of 1964-65 and for three complete seasons, 1965-66, 1967-68 and 1968-69. Post-breeding dispersal was studied only in 1965, 1968 and 1969. Study areas were selected to include diverse nesting habitats. On each of three main colonies a study area was pegged out which extended across the width of the colony so that it included peripheral and central nests. Other areas included groups of nests on high ground, on low ground and nests in newly established colonies. Each study area was normally visited daily throughout the breeding season.

3.1 Sex determination

Adults were sexed by a combination of bill measurements, depth at gonys and bill length. Depth at gonys was measured vertically from the point of inflection on the mandible to the upper edge of the premaxilla. Bill length was measured in a straight line from the tip to the outer edge of the gape.

The measurements from 165 dissected gulls are shown in Figure 2. To separate the sexes, a discriminant function analysis was calculated from the bill length and depth at gonys measurements. This gave the function, [(Length of Bill x 0.26012) + Depth at Gonys], with male values above and female below the point of discrimination at 22.875. With a 99% confidence interval the probability of error is less than 9.1%. In practice, however, the probability of error is much less because in most cases both partners are captured. Any gull which falls within the range of overlap may normally be correctly sexed when the mate is captured.

3.2 Banding operations

Annual banding of nestlings began at Kaikoura in the 1958-59 breeding season. Since then an estimated 40-60% of the chicks hatching each year have been banded (Table 2).

TABLE 2. Number of nestling Red-billed Gulls banded at Kaikoura

Season	No. banded	Progress total
1958-59	876	876
1959-60	2,229	3,105
1960-61	2,011	5,116
1961-62	2,031	7,147
1962-63	1,991	9,138
1963-64	2,062	11,200
1964-65	2,684	13,884
1965-66	3,403	17,287
1966-67	1,529	18,816
1967-68	1,240	20,056
1968-69	3,242	23,298

Irregular and less intense banding of chicks has been carried out in 35 localities throughout New Zealand and outlying islands (Appendix 1).

To identify individuals, colour banding was introduced in the 1967-68 season. All gulls captured breeding were sexed and given a single colour band, green or blue for males and white or yellow for females. If these were recaptured in the following season (1968-69) each was colour banded to

TABLE 3. Band characteristics and number of nestlings banded at Kaikoura

Band type	"A"	"B"	"C"	"D"	"E"	"F"
Band construction	butt to butt	butt to butt	butt to butt	clip	butt to butt	butt to butt
Band height (mm)	1.04	0.68	0.98	0.95	0.98	0.99
Band diameter (mm)	1.00	0.81	0.97	0.96	0.97	0.90
Band thickness (mm)	0.11	0.10	0.10	1.00	0.11	0.10
No. banded:						
1958-1959	876					
1959-1960	609	206	414	1,000		
1960-1961			-	2,011		
1961-1962			31	2,000		
1962-1963			1,991			
1963-1964			1,637		425	
1964-1965					2,684	
1965-1966					3,403	
1966-1967					1,529	
1967-1968					264	976
1968-1969						3,242
Total	1,485	206	4,073	5,011	8,305	4,218

Chemical composition of the bands:

Band type A.
Band type B. "Hard Aluminium"; composition unknown.

Band type C.
Band type D. "Pure Aluminium"; Copper 0.02%; Magnesium 0.02%; Manganese 0.01%; Silicon 0.05%; Iron 0.35%.

Band type E. "Hard Aluminium"; Copper 0.02-0.04%; Magnesium 1.80-2.40%; Manganese 0.27-0.33%; Silicon 0.10-0.18%; Iron 0.22-0.36%.

Band type F. "Monel"; Copper 27-32%; Nickel 66-70%; Iron 0.8-1.6%; Manganese 0.7-1.7%.

a known code.

3.3 Durability of bands and band loss

The unreliability of calculations based on band recoveries is well known (Hickey, 1952; Poulding, 1954; Coulson and White, 1955, 1959; Olsson, 1958; Harris, 1964a; Paynter, 1966; Rowley, 1966; Fordham, 1967; Ludwig, 1967; and Kadlec & Drury, 1968).

Band losses cause underestimates in computed population parameters because the number of potential recoveries is reduced. If banding data are to be used to investigate population dynamics with accuracy, it is necessary to know the life expectancy of the band. When the pattern of band loss has been determined it is possible to correct the raw data for it.

Another source of error results if the band inscription becomes indecipherable. Such bands are returned only if the finder has prior knowledge of where to send it. If they are returned it is often possible to read the number after treatment with graphite or acid.

It therefore became necessary to examine the durability of bands and band loss in the expectation of calculating correction factors or alternatively to recognise when a bias could influence the data.

Two different types of band, lock and butt to butt bands, have been used on Red-billed Gulls. Details of metal composition, dimensions and the number and years when each band type was used are given in Table 3.

Examination of the bands removed from gulls indicates that the greatest wear occurred on the internal surface. Since corrosion in salt water would affect both surfaces equally it is concluded that extra wear resulted from the

TABLE 4. Loss of bands from Red-billed Gulls

Band Type : A

	Number of years the band has been worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. gulls considered	-	-	-	-	3	8	9	10	13	18	1
No. of gulls that lost a band					0	1	0	1	3	10	0
Per cent lost					0	12.5	0	10.0	23.0	55.6	0
Cumulative per cent lost					0	12.5	12.5	21.2	39.6	73.1	73.1

Band Type : B

	Number of years the band has been worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. gulls considered	3	3	3	8	37	83	16	7	16	4	
No. of gulls that lost a band	0	0	0	0	1	3	2	1	4	2	
Per cent lost	0	0	0	0	2.7	3.6	12.5	14.3	25.0	50.0	
Cumulative per cent lost					2.7	6.2	17.9	29.6	57.2	78.6	

Band Type : D

	Number of years the band has been worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. gulls considered	-	-	-	5	19	27	80	119	74	14	6
No. of gulls that lost a band				0	0	0	1	2	1	0	1
Per cent lost				0	0	0	1.3	1.7	1.4	0	16.7
Cumulative per cent lost				0	0	0	1.3	3.0	4.4	4.4	20.4

Band Type : E

	Number of years the band has been worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. gulls considered	427	78	87	76	52	5	1				
No. of gulls that lost a band	0	0	0	0	0	0	0				
Per cent lost	0	0	0	0	0	0	0				
Cumulative per cent lost	0	0	0	0	0	0	0				

abrasion of the band against the leg. Any particles adhering to the surface of the leg would presumably assist the process.

The wear of lock bands was different from butt to butt bands. Wear on lock bands produces a characteristic notching at the base of, and also opposite to, the lock at the top of the band. Continual wear at these points is caused by the uneven weight distribution of the band which keeps the band tilted on the leg. The butt to butt bands, being evenly balanced, have the internal surface of the band worn uniformly. When the butt to butt bands are thin the ends open and the band falls off. Thin lock bands, however, are not lost from the bird until the notch enlarges and the band splits.

When the external surface of the band is severely worn the inscription becomes illegible. Appendix 2 shows the proportion of bands of different ages which had part of the inscription "SEND DOMINION MUSEUM WELLINGTON, NEW ZEALAND" erased. Lock bands were the only bands affected. Bands in this condition would seldom be returned to the authorities. When calculating mortality rates from dead recoveries reported by the public this would be an important source of error.

The number of bands falling off gulls during a known period of wear is shown in Table 4. Since 1966, it has been standard practice to add a second band to banded gulls recaptured alive. Later recovery of these rebanded gulls has allowed assessment of the significance of band loss. No bands were lost in the first four years of wear. After the fourth year the proportion lost differed for each type of band. It is unfortunate that the Ornithological Society of New Zealand discontinued the use of lock bands (Type D) as these are the best. Only 20.4% had been lost from gulls after ten years wear. For comparison, gulls with the butt to butt band (Type C) constructed of the same material as the lock band, had lost 78.6% of their bands by the tenth year.

Another high rate of loss (73.1%) was found for the largest butt to butt band (Type A). The "hard aluminium" (Type E) butt to butt bands have not been on long enough for adequate assessment of the rate of loss but none has been lost in the first six years of wear.

The loss of bands from males and females is shown in Appendix 3. The striking feature is the greater rate of loss of bands from females. A least squares analysis of the rate of band wear confirms that a faster rate of band wear occurred on female gulls (Figures 3 a, b, c). This aspect of band wear has not been considered by other researchers.

Band type E (Figure 3c) shows a constant rate of wear, but Types C and D (Figure 3 a, b) show a declining rate of wear after the fifth year. Ludwig (1967) found a similar decline in a sample of Ring-billed Gull Larus delawarensis bands, and concluded that the lighter bands were lost from the gulls after the fifth year and so they can not be recovered to be included in the sample, consequently the rate of wear shows an apparent decrease.

Since the greatest wear is caused by the movement of the band up and down the leg, two explanations for the different rate of wear are possible. Firstly, females may spend longer in habitats conducive to abrasion. In silty or sandy areas particles may adhere to the leg assisting abrasion. Secondly, the different rate of wear may be an "activity index". There is no evidence that females spend longer in sandy or silty habitats than males, but there is evidence to suggest that females are more active than males (see Section 4.2). In this regard many authors (Richdale, 1957; Perrins, 1965; and Brown, 1967b) believe that egg production places a great strain on the female than does sperm production on the male. Consequently, females may have to move about more to obtain the food necessary for egg production.

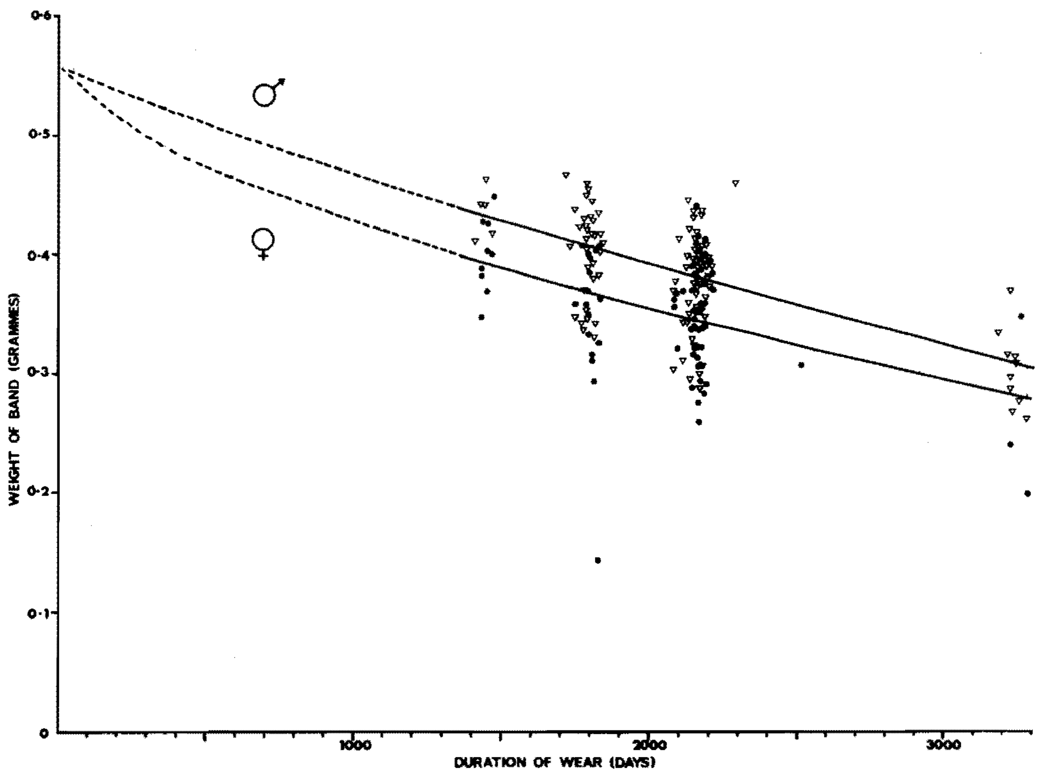

0·6
0·5
0·4
0·3
0·2
0·1
0
♂
♀
WEIGHT OF BAND (GRAMMES)
1000
2000
3000
DURATION OF WEAR (DAYS)

FIGURE 3a. Weight loss of band type C (butt to butt) worn by male and female Red-billed Gulls. (▽ males, ● females). Regression equations;

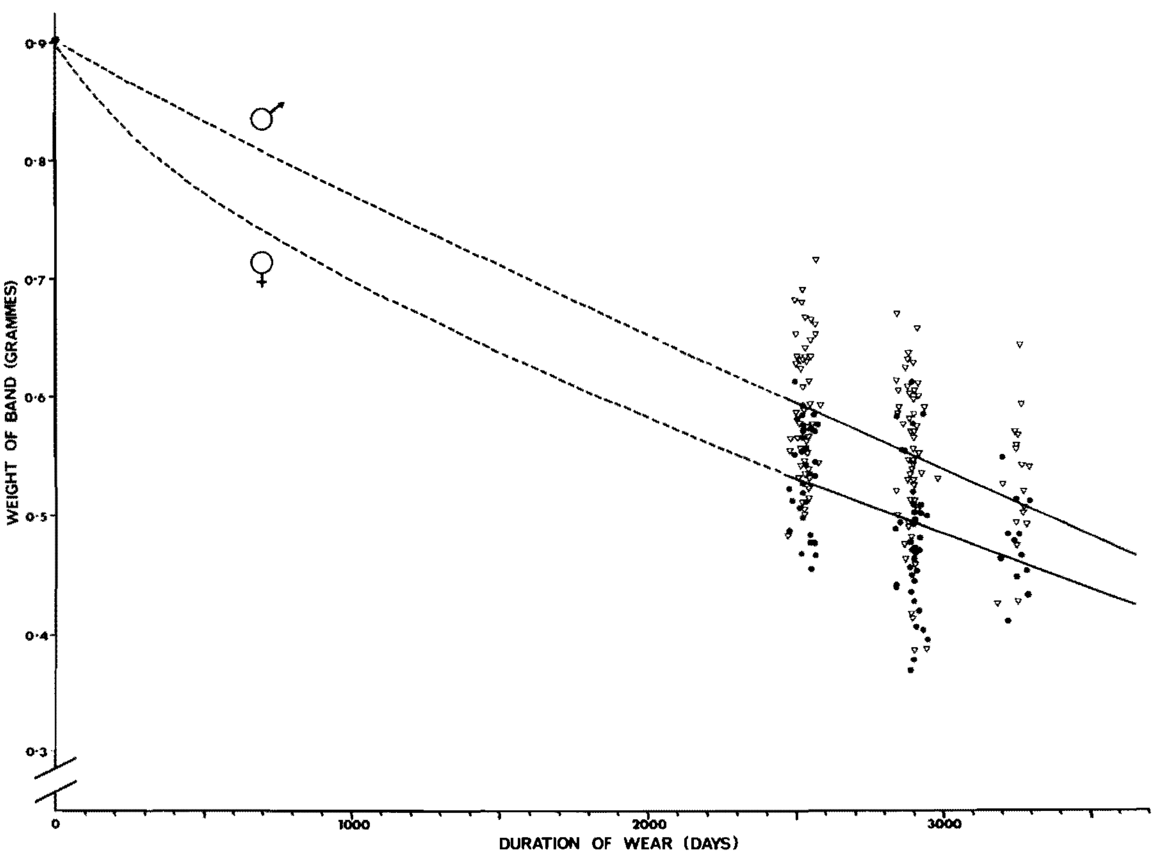
Females: Band weight =

Original band wt - 0.069(age in years x log 0.631)

Males: Band weight =

Original band wt - 0.036(age in years x log 0.889)

The original band weight (mean 0.5596 ± 0.0023) was calculated from 49 unused bands.



WEIGHT OF BAND (GRAMMES)
0·9
0·8
0·7
0·6
0·5
0·4
0·3
♂
♀
0
1000
2000
3000
DURATION OF WEAR (DAYS)

FIGURE 3b. Weight loss of band type D (lock connection) worn by male and female Red-billed Gulls. (∇ males, ● females). Regression equations:

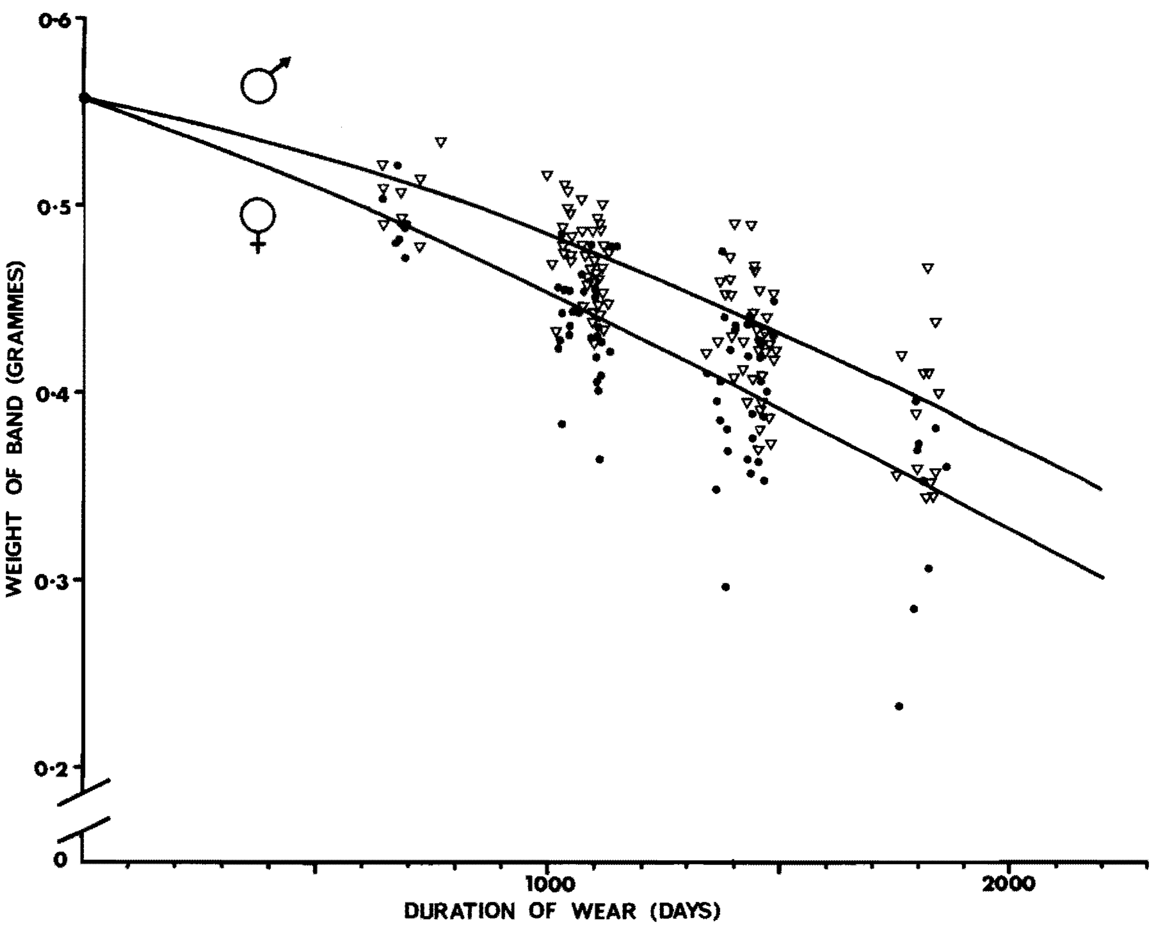
Females: Band weight =

Original band wt - 0.107(age in years x log 0.652)

Males: Band weight =

Original band wt - 0.053(age in years x log 0.915)

The original band weight (mean 0.9065 ± 0.0039) was calculated from 99 unused bands.



0·6
0·5
0·4
0·3
0·2
0
♂
♀
WEIGHT OF BAND (GRAMMES)
1000
2000
DURATION OF WEAR (DAYS)

FIGURE 3c. Weight loss of band type E (butt to butt) worn by male and female Red-billed Gulls. (▽ males, ● females). Regression equations:

Females: Band weight =

Original band wt - 0.032(age in years x log 1.155)

Males: Band weight =

Original band wt - 0.020(age in years x log 0.915)

The original band weight (mean 0.5562 ± 0.0265) was calculated from 51 unused bands.

3.4 Statistical analysis

Owing to variable numbers of chicks being banded each year at Kaikoura, each year class is corrected to 2,000 birds banded each year. At the commencement of this study it was hoped that correction factors for band loss could be devised to adjust recovery data. Unfortunately, the use of too many band types and the difference between sexes in the rate of band loss, has resulted in the sample sizes being too small for this purpose. It is hoped that correction factors can be devised later. The age structures, therefore, have not been corrected for band loss and so some of the older age classes are under-represented, especially females.

The statistical techniques follow methods outlined by Snedecor & Cochran (1967), and Sokal & Rohlf (1969). The level of significance is 0.05, unless otherwise stated.

3.5 Terminology and nomenclature

The ethological terms used follow Moynihan's (1955) nomenclature for the Black-headed Gull *Larus ridibundus* and subspecific names follow Peters (1934).

Other terms used in this thesis which require definition include:

a) "Recovery": a banded bird retrapped, seen or found dead at any place or time after banding (Kinsky, 1961).

b) "Recapture": a banded bird retrapped, seen or found dead after the first recovery.

c) "Breeding period": the period between the laying of the first egg at the colony and the fledging of the last chick.

d) "Pre-breeding period": the interim between the arrival of the birds at the colonies and the laying of the first egg at the colonies.

e) "Post-breeding period": the period between the fledging of chicks and the departure of the birds from the breeding grounds.

f) "Population": the "inhabitants of a particular area" (Elton, 1927).

g) "Breeding season": the time between the arrival of gulls at the breeding grounds until their departure.

h) "Established colonies": those which have had birds breeding consistently for at least five years.

i) "Newly established colonies": are colonies which have been established for less than three years.

j) "Adult": in adult plumage but has not necessarily bred.

k) "Juvenile": in immature plumage (6 weeks - 15 months).

l) "Breeding success": proportion of eggs producing fledged young.

3.6 Trapping procedures

Three methods were employed to trap adult gulls at the colonies. During incubation, adults were caught at the nest with an automatic drop-trap. The incubating bird returning to the nest disturbed a nylon line, causing a split peg supporting the trap to break, and the trap dropped. The time taken for the gull to enter the trap varied between ten seconds and three minutes, being shortest on cold days. Both sexes readily entered the trap and very few gulls failed to be caught.

A pole net, consisting of a five foot pole with a net on the end, was used on ledges and ridges where the drop trap could not be set. This method was also effective when chicks were in the nest, for adults were then reluctant to enter the nest if a drop-trap was present. Gulls returned to the nest immediately on release and little damage through trapping was experienced. It is believed that no bird deserted a nest as a result of handling.

Prior to and after breeding, gulls were captured by hand, on night roosts following illumination with a spotlight. The best results were achieved on calm, dry overcast nights.

3.7 Effects of investigator and visitors to colonies

Human intruders inevitably disturb nesting birds. In this study it was not possible to carry out field observations from a hide or blind and so some disturbance was unavoidable. The greatest harm resulted when adults were kept away from the nest. On these occasions neighbouring gulls usually devoured the eggs, and if large chicks were left they often wandered on to other territories and were severely pecked. This form of disturbance was minimised by moving slowly through the colonies since the adult gulls remained on or near the nest and so were able to protect their chicks and eggs against attack from other gulls.

When handling adults the drop-trap was left on the nest in such a way that no other gull could interfere with the nest and its contents.

Visitors frequently approach the gull colony at Lighthouse Point to visit the seals. Safe access to this colony can normally be made only an hour either side of low tide. At these times I was usually present and asked visitors not to disturb the gulls.

Disturbance during nest construction or site establishment may cause desertion particularly of inexperienced birds. Also, gulls nesting on the fringes of the colonies may be more susceptible to disturbance than those nesting in high density areas.

Considering all forms of disturbance it is believed that my presence caused very little desertion or loss of eggs and chicks by predation.

TABLE 5. Number of males and females captured in the prebreeding period according to age class

August 1965

Sex	Age in years 1	2	3	4	5	6	7
Male	2	7	11	9	8	9	4
Female	2	7	14	13	6	5	2
Total	4	14	25	22	14	14	6
P = (binomial expansion)	0.688	0.605	0.345	0.262	0.788	0.910	0.891

August - October 1968

Sex	Age in years 2	3	4	5	6	7	8	9	10
Male	8	34	22	11	11	12	10	8	4
Female	8	26	21	15	10	15	13	8	0
Total	16	60	43	26	21	27	23	16	4
P = (binomial expansion)	0.598	0.877	0.620	0.279	0.416	0.351	0.339	0.598	0.063

4. SEX RATIO

Samples of banded gulls obtained at different times of the year showed considerable differences in the sex ratio.

4.1 Sex ratio prior to and at breeding

The samples of banded gulls captured in the pre-breeding period by spotlighting on night roosts are shown in Table 5. The sex ratio in all age classes did not differ significantly from an expected 50:50 ratio. However, in the samples of banded gulls captured during incubation by pole netting and drop-trapping there was a preponderance of males (Table 6). Many age classes showed a significant deviation from an expected 50:50 sex ratio.

Spotlighting does not favour the recovery of either sex since most gulls illuminated were readily captured. Similarly, the discrepancy in the sex ratios between the pre-breeding and breeding samples cannot result from disproportionate emigration of males as those seen elsewhere (Wellington, Lyttelton and Christchurch) during the pre-breeding period were accompanied by their future mates. It was assumed (Mills, 1967) that the disproportionately large number of banded males captured in the breeding population represents a trapping bias. To account for this it was postulated that males undertake a greater share of the incubation and would therefore be more likely than females to be captured. However, more recent study has shown that no trapping bias exists. Tasker (1970) found that there was no significant difference between males and females in the time spent in the nest territory during incubation.

In the 1967-68 breeding season an attempt was made to capture all banded gulls breeding in study areas. All gulls

TABLE 6. Number of males and females captured in the breeding season

1964-65

Sex	Age in years				
	2	3	4	5	6
Male	41	35	58	61	31
Female	13	26	23	26	13
Total	54	61	81	87	44
Note.					
$p(X^2)$	0.01	0.5	0.005	0.001	0.005

1965-66

Sex	Age in years					
	2	3	4	5	6	7
Male	18	58	44	77	76	49
Female	4	51	44	51	43	27
Total	22	109	88	128	119	76
Note.						
$p(X^2)$	0.05	0.75	0.5	0.1	0.05	0.1-0.05

1967-68

Sex	Age in years							
	2	3	4	5	6	7	8	9
Male	17	24	40	56	45	64	47	16
Female	2	14	24	42	32	54	29	14
Total	19	38	64	98	77	118	76	30
Note.								
$p(X^2)$	0.01	0.25	0.1	0.5	0.25	0.5	0.25	0.5

1968-69

Sex	Age in years								
	2	3	4	5	6	7	8	9	10
Male	4	35	37	58	74	60	60	55	25
Female	0	8	26	26	52	49	47	34	14
Total	4	43	63	84	126	109	107	89	39
Note.									
$p(X^2)$	0.25	0.005	0.25	0.01	0.25	0.5	0.5	0.1	0.25

captured were given a single colour band and rebanded with a new metal band as a precaution against loss of bands. This meant that within the population there was a known number of banded males and females which were known to breed. If a trapping bias existed, it was expected that when these gulls were recaptured the following breeding season a significantly higher proportion of males would be recovered. As this was not so there can be no trapping bias (Table 7).

TABLE 7. Proportion of banded males and females recaptured breeding in successive seasons (1967-68 & 1968-69)

	No. banded gulls recovered in 1967-68	No. banded gulls recaptured in 1968-69
Males	320	210 (65.6%)
Females	204	121 (59.3%)

Note. Fisher's exact test $p = 0.1698$

Fitting colour bands could not have increased the possibility of recapturing a female rather than a male. Nor could loss of colour bands be considered a contributing factor as they showed minimal wear and no banded bird was recovered with a colour band missing. Since the recapture data show that there is an equal chance of recovering a banded male or female during the incubation period, the sex ratio in the recovered birds of each age group breeding must be considered to be representative of that year class which is breeding (except in the

TABLE 9. Proportion of banded males and females in the pre-breeding population

	Males	Females
Number captured	31	33
Number banded	19	14
Per cent banded	61.3%	42.4%
Per cent not banded	38.7%	57.6%

Note. Fisher's exact test $p = 0.20765$

TABLE 10. Proportion of unknown aged new partners breeding with males and females that changed mates

Sex	No. changing mates	New breeding partner	
		Unknown age	Known age
Male	28	19 (67.9%)	9 (32.1%)
Female	24	14 (58.3%)	10 (41.7%)

Note. Fisher's exact test $p = 0.67224$

older age classes where females lose more bands).

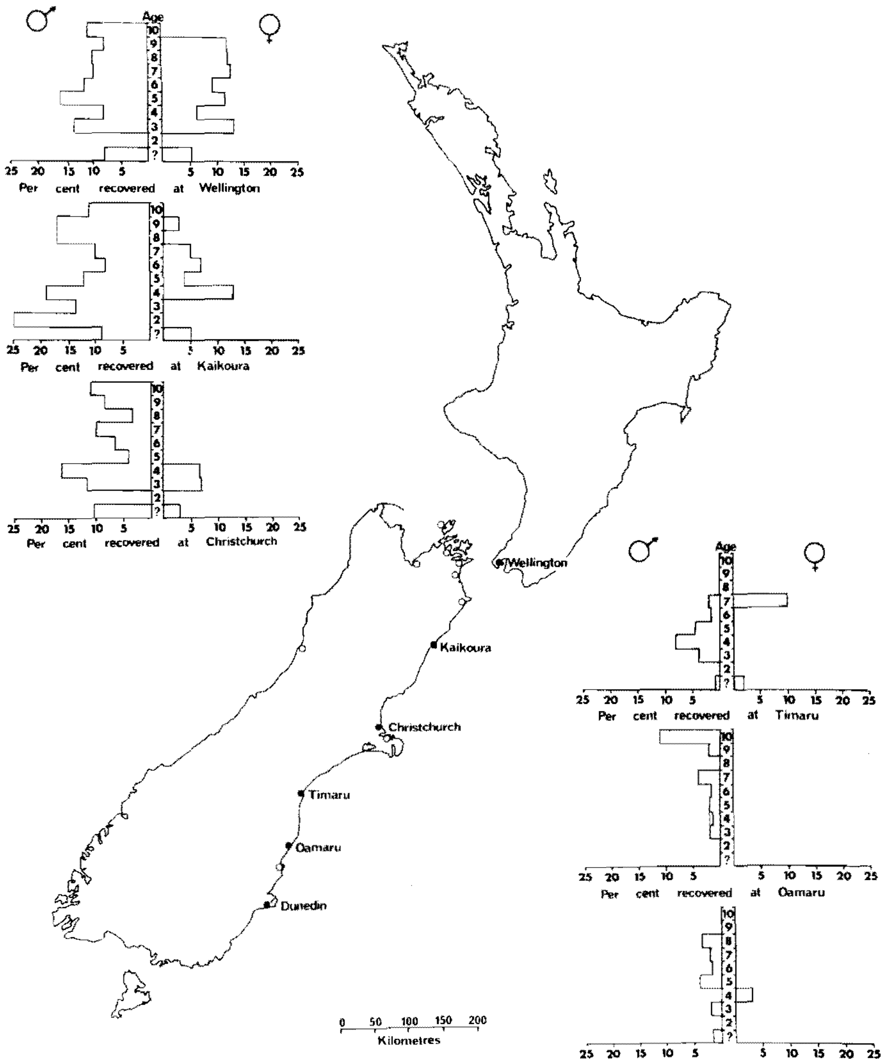
It is now concluded that fewer banded females than banded males are captured because female survival is greater in the cohorts not banded (gulls over 10 years of age). This results in a greater proportion of unbanded females in the population; this shows clearly in the records of partners of banded males and females captured in the 1967-68 and 1968-69 breeding seasons (Table 8). In both breeding seasons significantly

TABLE 8. Proportion of known aged males and females breeding with unknown aged partners

Season	Sex	No. of known age	Breeding partner	
			unknown age	known age
1967-68				
	Male	183	108 (59.0%)	75 (41.0%)
	Female	126	51 (40.5%)	75 (59.5%)
1968-69				
	Male	305	208 (68.2%)	97 (31.8%)
	Female	195	98 (50.3%)	97 (49.7%)

Note. Fisher's exact test (1967-68) $p = 0.00195$
Fisher's exact test (1968-69) $p = 0.00009$

more unbanded partners were breeding with banded males than with banded females ($p = < 0.001$). This shows clearly a surplus of unbanded females in the population. Additional support for this contention, although not statistically significant, is shown by the excess of unbanded females in the



Age
Per cent recovered at Wellington
Per cent recovered at Kaikoura
Per cent recovered at Christchurch
Wellington
Kaikoura
Christchurch
Timaru
Oamaru
Dunedin
Kilometres
Per cent recovered at Timaru
Per cent recovered at Oamaru
Per cent recovered at Dunedin

FIGURE 4. Percentage of colour marked males and females seen at different localities between 1 May and 30 June 1968.

pre-breeding population (Table 9) and the greater proportion of males than females with unbanded new partners following a change of mate (Table 10).

4.2 Sex ratio following dispersal

The sex ratio in the non-breeding period was determined from recoveries of gulls that were sexed and colour marked in the previous breeding season. Figure 4 and Table 11 show the proportion of males and females seen at different areas. The number of gulls recovered in the two years differed being higher in 1969 because birds were individually colour coded and could be identified from a distance whereas this was not so in 1968. Significantly more males than females were recovered in all areas. The small numbers of females recovered can not be attributed to mortality since recoveries of colour marked gulls breeding at Kaikoura indicate that a large proportion survived from the previous breeding season (Table 7). This suggests that males are more easily seen than females outside of the breeding season, perhaps because females move around more. Alternatively, females may tend to feed offshore more than males. Stonehouse (1965) has recorded flocks of seagulls feeding at sea between Cape Campbell and Pegasus Bay in May and July.

Analysis of the recapture data (Figure 5 and Table 12) shows that the distribution of recaptures of both sexes, with the exception of males in Christchurch, does not depart significantly from the expected Poisson distribution. In the analysis the first recapture was treated as the original marking, the second recapture as the first recapture and so on. Although there is a tendency for the recapture data to consist of too many individuals not recaptured and too many recaptured frequently, the recovery data at Wellington, Kaikoura, Timaru,

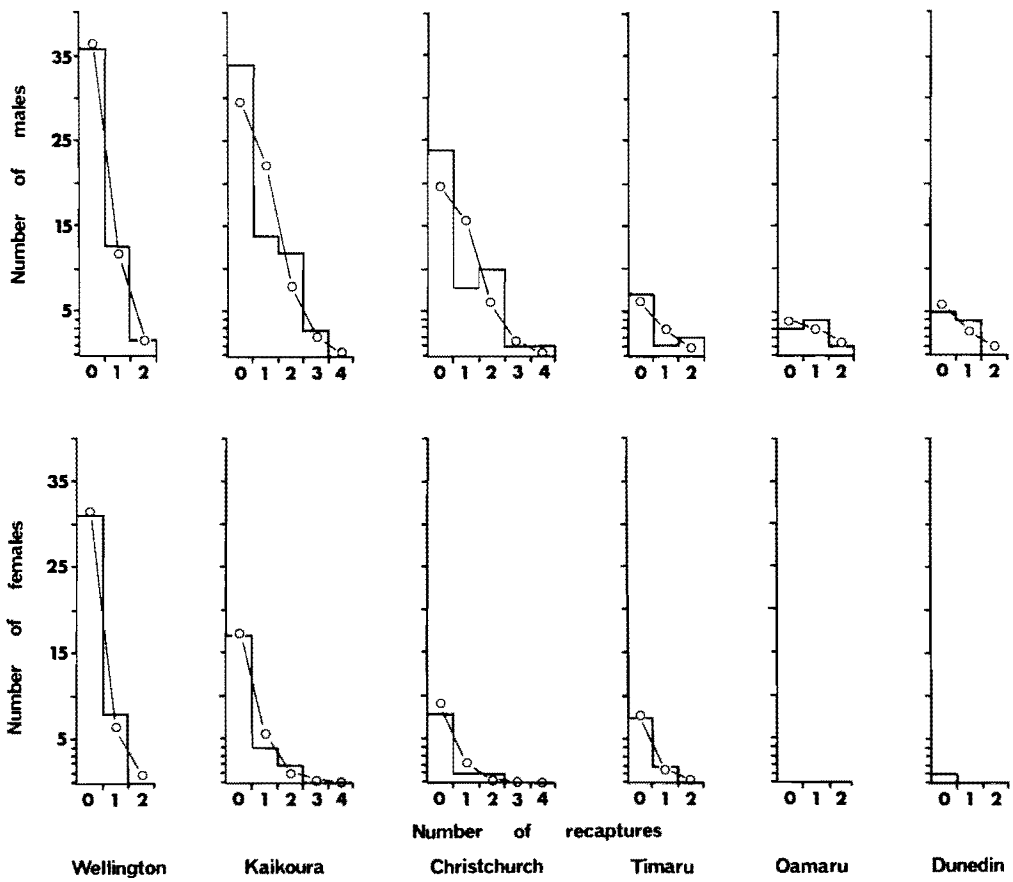

Number of males
Number of females
Number of recaptures
Wellington
Kaikoura
Christchurch
Timaru
Oamaru
Dunedin

FIGURE 5. Distribution of recaptures in relation to the expected Poisson distribution.

TABLE 11. Recoveries of colour marked Red-billed Gulls at different localities in winter

	1967				1968			
	Males		Females		Males		Females	
No. colour marked gulls available	395		342		506		490	
	No. seen	% seen	No. seen	% seen	No. seen	% seen	No. seen	% seen
Wellington	18	4.6%	6	1.8%	51	10.1%	39	8.0%
Nelson	0		0		2	0.4%	0	
Havelock	0		1	0.3%	1	0.2%	3	0.6%
Picton-Blenheim	1	0.2%	1	0.3%	1	0.2%	0	
Kaikoura	32	8.1%	8	2.3%	62	12.3%	24	4.9%
Christchurch	24	6.1%	2	0.6%	44	8.7%	10	2.0%
Lyttelton	-	-	-	-	2	0.4%	1	0.2%
Timaru	5	1.3%	2	0.6%	10	2.0%	9	1.8%
Oamaru	6	1.5%	0		8	1.6%	0	
Moeraki	1	0.2%	0		1	0.2%	0	
Dunedin	4	1.0%	0		9	1.8%	1	0.2%
Invercargill	0		0		-	-	-	-
Greymouth	0		0		0		0	

Oamaru and Dunedin are sufficiently random (Table 12) to allow application of Jolly's (1965) stochastic model to compute the population size. Among other things, Jolly's model has the advantage over other methods as the trapping efforts are not required to be equal on each occasion and there is no need for the intervals between trapping periods to be equal (Williams, 1965; Manly & Parr, 1968). Although more males were recovered at Kaikoura the estimates of population size of the

TABLE 12. Comparison of recapture distributions with corresponding Poisson distribution

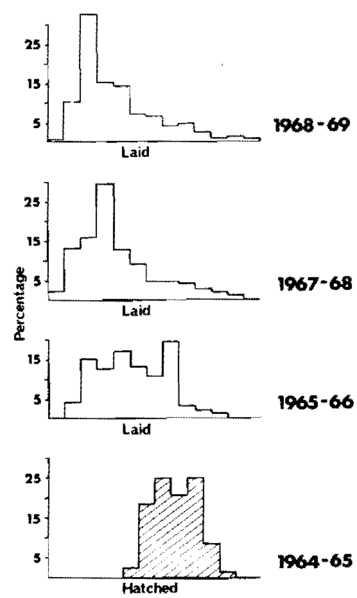
	Males			Females		
Locality	G-test statistic	d.f.	p	G-test statistic	d.f.	p
Wellington	0.554	1	0.50-0.25	1.766	1	0.25-0.10
Kaikoura	6.807	3	0.10-0.25	1.629	3	0.75-0.50
Christchurch	8.682	3	0.05-0.025	1.829	3	0.75-0.50
Timaru	3.668	1	0.10-0.05	0.482	1	0.50
Oamaru	1.249	1	0.50-0.25			
Dunedin	2.122	1	0.25-0.10			

sexes are the same for 16 and 17 May (Table 13). In Wellington, the estimates gave more females than males. This supports the view that the ratio of females to males is greater than was observed but females are less readily seen.

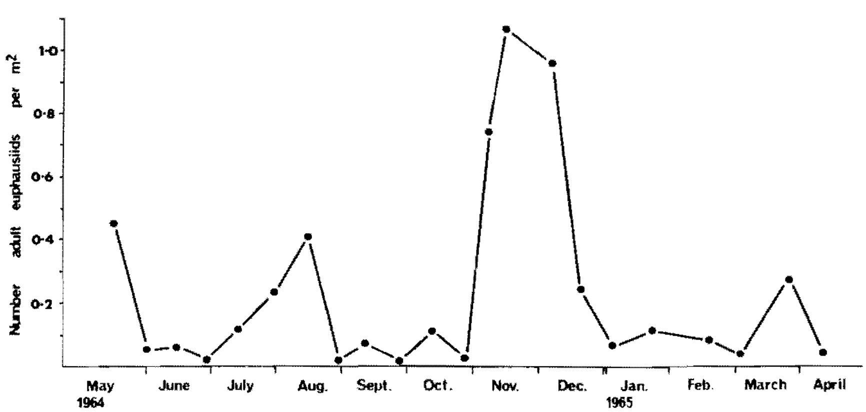
TABLE 13. Estimates of population size of males and females from the Kaikoura population at different localities in winter 1968

Locality	Date	Males		Females	
		N	S.E.	N	S.E.
Wellington	20 June	29.7	7.8	58.7	60.6
Kaikoura	15 May	81.6	114.7	132	*
	16 May	39.4	4.6	40.0	38.8
	17 May	52.6	15.3	60.0	76.5
Christchurch	21 May	67.1	34.5	*	*
	22 May	31.9	4.6	4.0	*
Timaru	4 June	*	*	4	*
Oamaru	10 June	*	*	*	*
Dunedin	7 June	21.0	24.1	*	*

Note. * number of recaptures small so no estimate can be made.



Percentage
25
15
5
1968-69
Laid
1967-68
Laid
15
5
1965-66
Laid
1964-65
Hatched



Number adult euphausiids per m^2
1·0
0·8
0·6
0·4
0·2
May 1964
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan. 1965
Feb.
March
April

FIGURE 6. Relative abundance of adult euphausiids (after Grieve, 1966) and the hatching and laying periods of the Red-billed Gull.

PLATE 1. Aerial view of gulls feeding with fish shoals. The gulls are feeding on the periphery of the shoals, presumably on the planktonic euphausiid Nyctiphanes australis which the fish are believed to be feeding on also.

5. BREEDING CYCLE

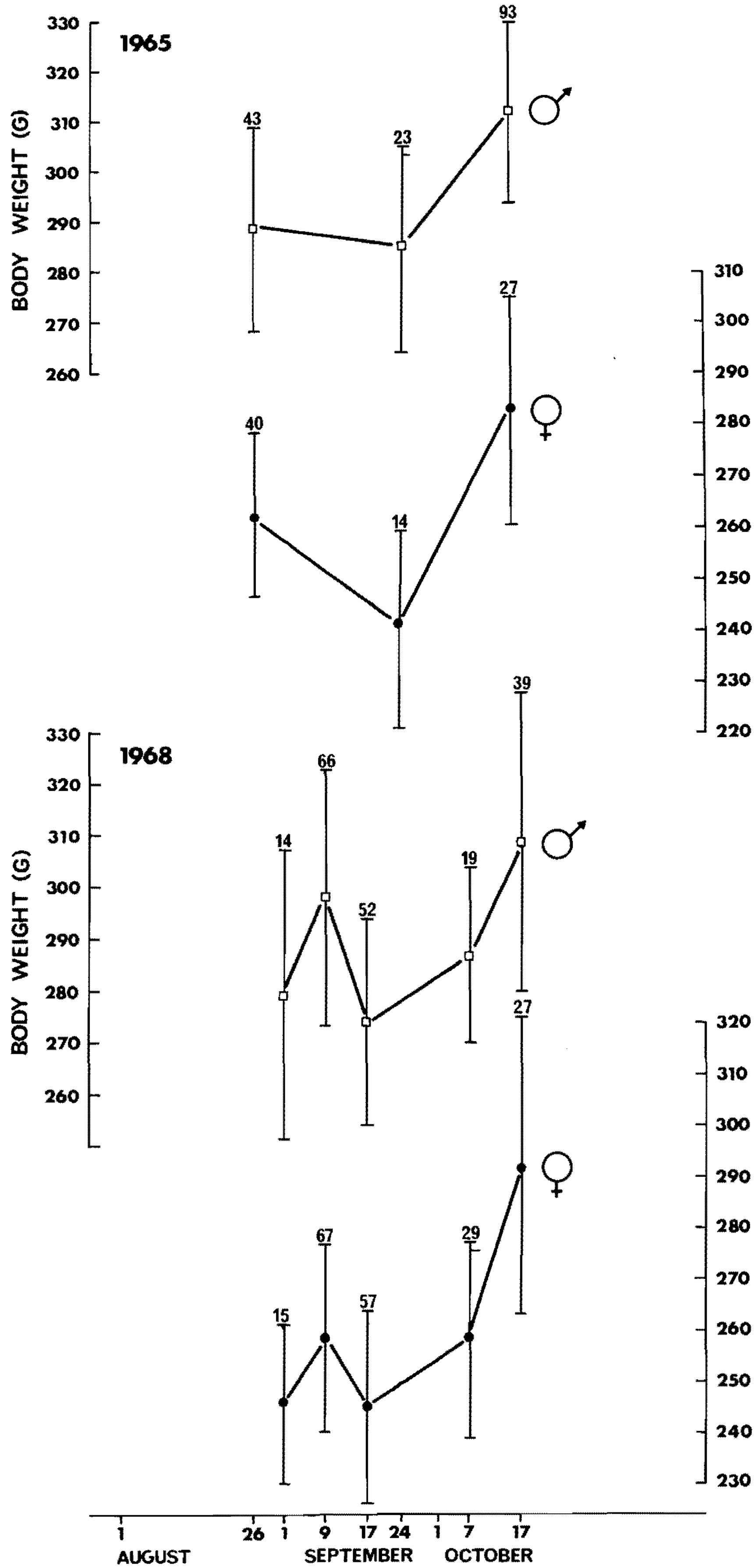
5.1 Period of food abundance

The diet of breeding adult gulls and nestlings consists chiefly of the planktonic euphausiid *Nyctiphanes australis*. Comparison of the relative abundance of adult euphausiids in 1964 and 1965 (after Grieve, 1966) and the number of chicks hatching in the 1964-65 breeding season (Figure 6) shows that the peak abundance of adult euphausiids coincides with the hatching period. The laying periods of subsequent seasons are also given. It must be emphasised that the relative abundance of adult euphausiids does not represent the availability, since the Euphausiacea, to which *N. australis* belongs, normally lives in detritus-bearing waters near the bottom of the continental shelf, feeding on copepod faecal pellets and live diatoms and are found at the surface only for brief periods (Sheard, 1953). At Kaikoura, Grieve (1966) invariably found Euphausiacea at the surface, but the maximum concentration of all stages was found between 22 and 100 metres depth. For brief periods in its life history *N. australis* forms swarms at the surface (Sheard, 1953) and it is then that it is available to gulls (Plate 1). Stonehouse (1965) recorded flocks of 2,000 gulls associated with such swarms, and smaller flocks totalling several thousand birds occurring simultaneously along many miles of coast.

The reasons for swarm formation are not known (Mauchline & Fisher, 1969). Sheard (1953) contends that adult *N. australis* swarm for breeding, and masses of larvae either congregate over a period in local rips and eddies or are released in "floods" during brief mass-hatching periods. Komaki (1967) suggests that the surface swarms of *Euphausia pacifica* in Japanese waters are associated with cold water masses, and the mixing of these with warmer coastal water produces the swarms, usually at the margins of the cold masses. Similarly, Murphy & Shomura (unpublished manuscript, quoted by Ashmole & Ashmole, 1967) emphasise the importance of "fronts" in concentrating plankton into small areas. According to Voorhis & Hersey (1964) a front is detected by abrupt changes in the surface temperature. Many of the fronts which develop are associated with convergence and sinking (Uda, 1938; Cromwell & Reid, 1956; Knauss, 1957). Ashmole & Ashmole (1967) pointed out that the biological significance of such fronts is that "they tend to concentrate plankton species which are capable of resisting the downward currents".

Some species of euphausiids form temporary swarms prior to breeding; others, however, such as Euphausia surperba, form subpopulations in the larval stages and remain aggregated (Mauchline & Fisher, 1969; Marr, 1962). It is not known whether Nyctiphanes australis swarms are permanent or temporary. The extent of N. australis swarms vary. Fishermen (pers. comm.) at Kaikoura have encountered small swarms with a patchy distribution and others two acres in extent and a metre in depth. The number of euphausiids present in some swarms is enormous. In a swarm of Euphausia krohnii off the Canary Islands, the density was estimated to be 30,000 per cubic metre (Baker, quoted by Mauchline & Fisher, 1969).

Although there appears to be an abundance of N. australis at Kaikoura, the plankton is only available when it swarms at the surface. Furthermore, the euphausiids are subject to fluctuations in abundance caused by hydrological disturbances (Grieve, 1966). In December 1964 and January 1965 a marked reduction of numbers coincided with an influx of oceanic water. Associated with the disappearance of euphausiids, Grieve noted a similar disappearance of Kahawai Arripis trutta, which rely on euphausiids for a greater part of their diet. For these reasons, the plankton off the Kaikoura coast may not be avai-



1965
1968
BODY WEIGHT (G)
BODY WEIGHT (G)
330
320
310
300
290
280
270
260
220
230
240
250
260
270
280
290
300
310
320
43
23
93
40
14
27
14
66
52
19
39
15
67
57
29
27
♂
♀
1
26
1
9
17
24
1
7
17
AUGUST
SEPTEMBER
OCTOBER

FIGURE 7. Seasonal variation of body weight of adult Red-billed Gulls. The mean and one standard deviation from the mean are given.

lable to the gulls at all times. This unreliability of the food supply may be a limiting factor for the breeding population. When the swarms appear, competition for food probably develops.

The change in mean body weight of gulls in the prebreeding period indicates that food during this period is in short supply (Figure 7). In 1965 the gulls quickly lost weight from the time of their arrival at Kaikoura in August until the end of September. In 1968 the loss of weight occurred in September. According to Grieve (1966), the availability of adult euphausiids does not reach a peak until November, so the weight decline is probably caused by keen competition for a relatively restricted food supply. The mean weight of the sample of males and females for the 7 October 1968 are statistically lower than the mean weights of the sample of males and females trapped between 10 and 17 October (Table 14). The samples of 7 October are from the whole colony,

TABLE 14. Mean weights of male and female Red-billed Gulls prior to and at breeding in 1968

Date	Male			Female		
	No. gulls	Mean	S.D.	No. gulls	Mean	S.D.
7 October	19	287.9	17.18	29	258.0	19.42
10-17 October	39	309.9	20.28	27	292.0	29.49
Per cent increase		7.1%			11.6%	
	$t = 4.0378$, d.f. $= 56$, $p = < 0.001$			$t = 5.0353$, d.f. $= 54$, $p = < 0.001$		

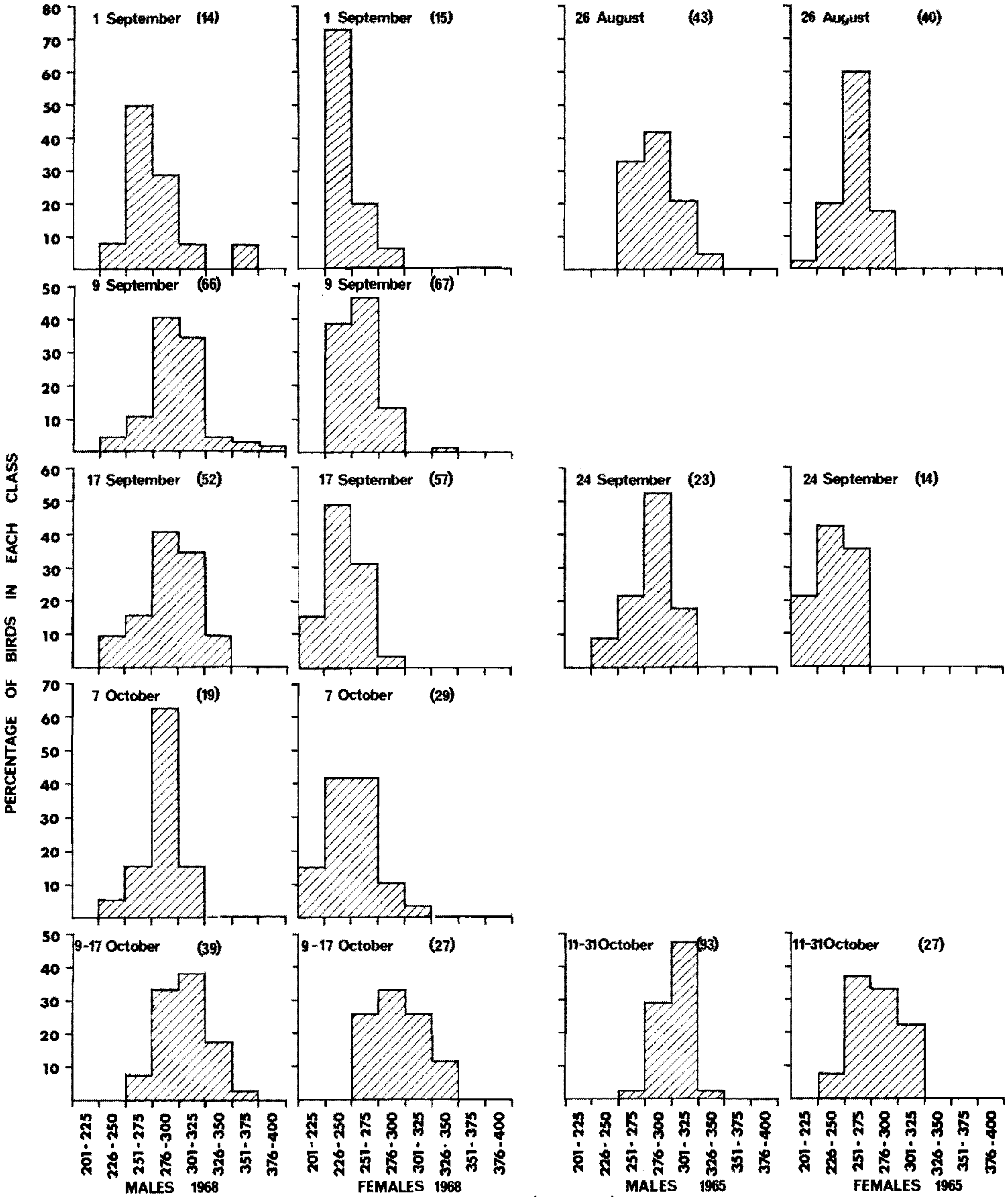

1 September (14)
1 September (15)
26 August (43)
26 August (40)
9 September (66)
9 September (67)
17 September (52)
17 September (57)
24 September (23)
24 September (14)
7 October (19)
7 October (29)
9-17 October (39)
9-17 October (27)
11-31October (93)
11-31October (27)
PERCENTAGE OF BIRDS IN EACH CLASS
201-225
226-250
251-275
276-300
301-325
326-350
351-375
376-400
MALES 1968
FEMALES 1968
MALES 1965
FEMALES 1965
WEIGHT (GRAMMES)

FIGURE 8. Variations in the frequency distribution of male and female body weight.

TABLE 15. Mean body weight of male and female Red-billed Gulls of known age in the pre-breeding period of 1968-69

Age in years	Males						Females					
	7 September			17 September			7 September			17 September		
	No.	Mean	S.D.	No.	Mean	S.D.	No.	Mean	S.D.	No.	Mean	S.D.
2				5	275.0	15.4				7	249.3	12.1
3	15	299.7	30.8	17	263.8	20.1	9	258.3	15.6	17	238.8	15.6
4	9	290.0	10.9	10	269.0	19.4	10	256.0	11.5	11	250.5	25.5
5-10	30	299.5	27.6	22	281.1	19.1	19	259.7	23.0	24	251.7	16.8

Note. t(between 3 & 5-10yr females, 7 Sept.) = 0.1659, d.f. = 26, p = 0.50
t(between 3 & 5-10yr males, 7 Sept.) = 0.0187, d.f. = 43, p = 0.50
t(between 2 & 5-10yr females, 17 Sept.) = 0.3479, d.f. - 29, p = 0.50
t(between 2 & 5-10yr males, 17 Sept.) = 0.6664, d.f. = 25, p = 0.50
t(between 3 & 5-10yr females, 17 Sept.) = 2.4871, d.f. = 39, p = 0.025
t(between 3 & 5-10yr males, 17 Sept.) = 2.7405, d.f. = 37, p = 0.01
t(between 4 & 5-10yr males, 17 Sept.) = 1.6558, d.f. = 30, p = 0.10

taken three days before the laying commenced at Kaikoura, while the samples taken between 10-17 October are restricted to the earliest breeders. The same trend is noted in 1965, but in this case the sample of 17 October is of gulls captured breeding throughout October (Figure 7). The substantial difference in mean weight between the early breeders and the general population indicates that early breeders are the gulls which have competed most successfully for food, and that the others require more time to attain breeding condition. The weight distributions of the breeding population (Figure 8) show an absence of light gulls which are known to be present in the general population. It is a reasonable assumption that these have not reached breeding condition. This is in agreement with the argument put forward by Perrins (1965) which suggests that females commence breeding at the earliest time they are able to attain breeding condition. It must be emphasised that these early breeders have attained breeding condition prior to the increase in food abundance; this is an advantage since these gulls will have chicks in the nest when food becomes plentiful.

Table 15 shows that there is no statistical difference in the mean weights of male or female gulls of different ages at 7 September. On 17 September the mean weights of three year old males and females are statistically lighter than for gulls over four years of age. These observations show, as Lack (1954) has pointed out, that at the time when the population is facing food shortage not all individuals in the population are affected. Younger gulls are most affected at these times, however, it must be noted that the variability of weights within all age classes is large.

Ward (1965b), quoting Connell _et al_ (1960), concludes "that as a rule changes in body weight of adult birds are the result of changes in the fat reserves, though this may not apply when starvation is acute and tissues other than fat are broken down, or in females producing eggs". Table 16 summarises the fat content of known aged gulls in the pre-breeding period. The fat was dissected away from the body wall and the periviscera. There is a trend for two and three year old gulls to have less fat reserves than older gulls.

TABLE 16. Fat reserves (grammes) of known aged gulls in the pre-breeding period of the 1968-69 season

Date	2-3 year gulls			4-10 year gulls		
	No. gulls examined	Sub-cutaneous fat	Peri-visceral fat	No. gulls examined	Sub-cutaneous fat	Peri-visceral fat
MALES						
17 Sept.	10	1.79±1.82	0.78±0.71	6	4.38±3.23	1.30±0.80
7 Oct.	8	3.78±3.90	1.08±1.40	9	4.09±2.24	1.08±0.85
FEMALES						
17 Sept.	9	4.80±2.10	1.68±0.69	7	3.26±2.55	1.36±1.25
7 Oct.	9	3.61±2.15	1.12±0.84	9	6.22±3.88	2.12±1.62

5.2 Return to the colonies and occupation of nest sites

The gulls begin to arrive at Kaikoura in late June, having been away since January, but the occupation of prospective nest sites does not begin until early August. In the interim the gulls show no apparent interest in the traditional nesting colonies, spending the day feeding along the coast and the night roosting on offshore islands (Mills, 1967). It is not

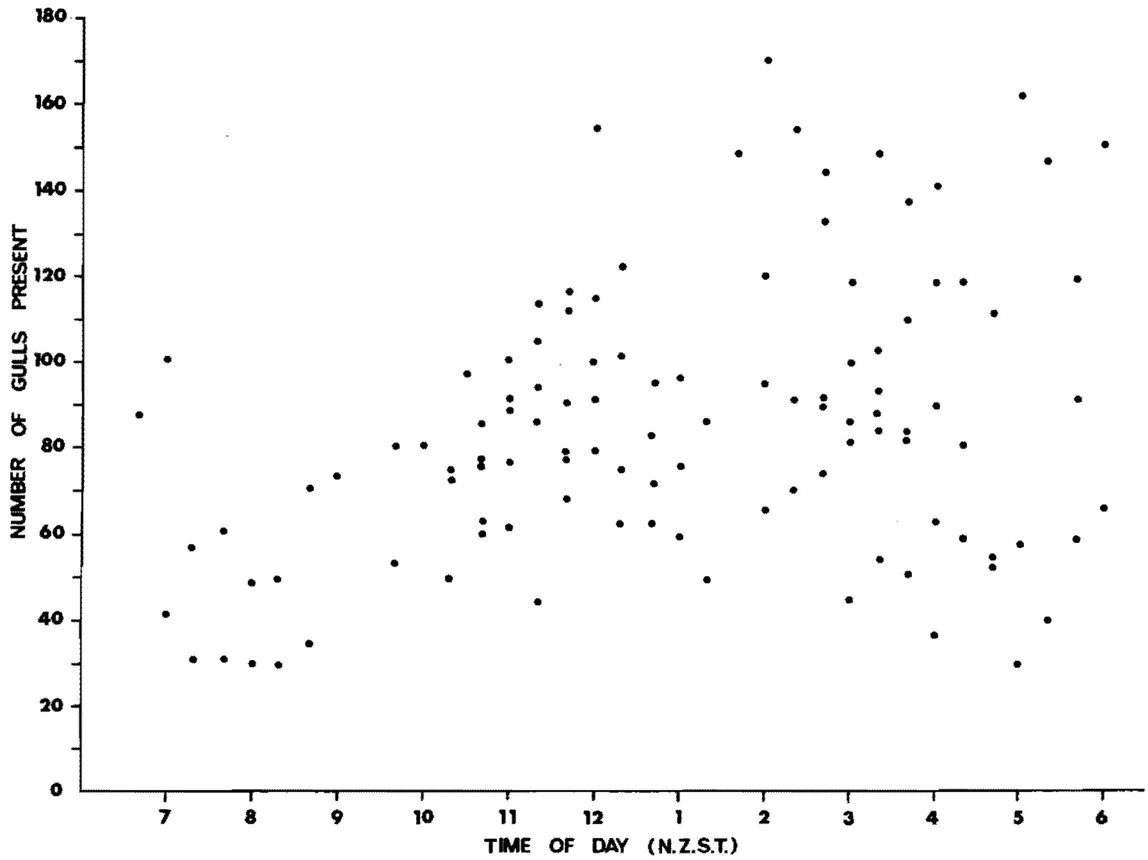

NUMBER OF GULLS PRESENT
0
20
40
60
80
100
120
140
160
180
7
8
9
10
11
12
1
2
3
4
5
6
TIME OF DAY (N.Z.S.T.)

FIGURE 9. Diurnal variations in the number of Red-billed Gulls in a colony study area prior to egg laying.

until late August or early September that the nesting colony is occupied at night as well as day. This may be to counter night attacks by Stoats, Mustela erminea. The Black-headed Gull Larus ridibundus at Ravenglass, England, was also reluctant to roost at night on nesting colonies prior to breeding because of the presence of Foxes Vulpes vulpes (Kruuk, 1964; Tinbergen, 1967).

The first areas claimed are usually the elevated portions of the colonies. Throughout the prelaying period, the number of gulls occupying nest sites fluctuates during the day (Figure 9). Peaks of occupancy occur early in the morning, at mid-day and in the early afternoon. Table 17 shows that there is a marked reduction in the time the territory is

TABLE 17. Temporal relationships of paired gulls with the territory in the pre-incubation period. (After Tasker, 1970)

Date*	Observation time+	Time female present	Time male present	Time together	Time both absent
-13 to -20	16.50	10.04(60.8%)	4.09(24.8%)	2.33(14.1%)	5.10(30.9%)
- 7 to -12	44.30	37.59(84.9%)	14.18(32.0%)	9.52(21.5%)	2.05(4.6%)
- 1 to - 6	51.30	44.01(85.8%)	21.39(41.7%)	14.13(27.5%)	0.03(0.06%)
Total time	112.50	92.04(81.8%)	40.06(35.6%)	26.38(23.4%)	7.18(6.4%)

Note. * Day -1 is the day before the first egg is laid.
+ Time is in hours and minutes.

occupied as the egg-laying date approaches. Table 17 also shows that females spend over twice as long in the territory than do males; Tasker (1970) found the difference to be significant ($p = 0.001$).

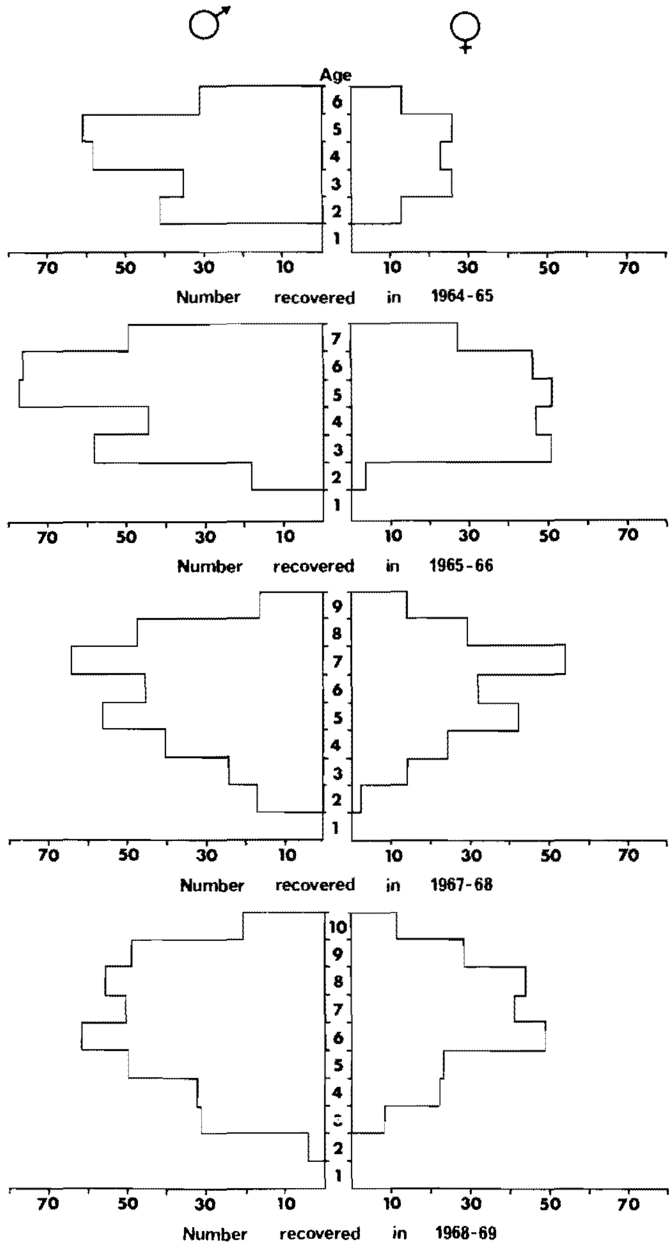
5.3 Return tendency

Despite banding of chicks at 31 localities throughout New Zealand less than 1% of the banded gulls recovered breeding were banded at localities other than Kaikoura (Table 18). All the "foreign" banded gulls recovered breeding were fledged at Lake Grassmere, 82 miles north of Kaikoura.

TABLE 18. Locality of banding of the banded gulls recovered breeding at Kaikoura

Locality of banding as chicks	1967-68		1968-69	
	Males	Females	Males	Females
Kaikoura	325	211	279	236
Lake Grassmere	2	3	3	2
Total	327	214	382	238

Males tend to breed at their natal colony (philopatry) but this trait is not so marked in female gulls (Table 19). The proportion of males recovered breeding at the natal colony is high considering that there are three large and seven small colonies where the males could breed. Philopatry has also been described for the Shag *Phalacrocorax aristotelis* (Potts, 1969), the Gannet *Sula bassana* (Nelson, 1966b) and the Short-



♂
♀
Age
Number recovered in 1964-65
Number recovered in 1965-66
Number recovered in 1967-68
Number recovered in 1968-69
70 50 30 10 10 30 50 70

FIGURE 10. Number of males and females of known age recaptured breeding at Kaikoura.

TABLE 20. Age of breeding partners

Age of females (years)	Age of male (years) 2	3	4	5	6	7	8	9	10	Mean of male
2	2									2.00
3	7	13	3	1	1					3.04
4	2	11	9	5	2	1	1			4.03
5	1	3	9	12	4	3	1			4.85
6	1	6	7	13	6	4		1		4.89
7	1	4	4	6	13	4	4	2		5.68
8		2	2	2	4	9	5	2		6.50
9		1	1	2	1	3	3	4	1	7.13
10		1						2		7.00
Mean of female	3.64	4.80	5.29	5.78	6.42	7.08	7.43	8.36	9.00	

Note. Percentage with partners the same age = 25.9%

Percentage with the male being older = 17.0%

Percentage with the female being older= 57.1%

tailed Shearwater *Puffinus tenuirostris* (Serventy, 1967).

TABLE 19. The relation of natal and breeding colony

Breeding and natal colony	1967-68		1968-69	
	Males	Females	Males	Females
Same	15	2	26	6
Different	16	8	33	10

5.4 Sex differences in the age at first breeding

With a large breeding population it is impossible to be sure at what age birds breed for the first time. However, it is evident from the age composition of banded gulls captured breeding over four seasons that the age of first breeding is variable (Figure 10). The gulls are capable of breeding at two years of age, but the majority breed for the first time at three, four and five years and some even later. The proportion of young birds in the population in the 1964-65 season is exaggerated because sampling of the breeding population commenced late in the season when proportionately more young gulls are breeding.

The striking feature of Figure 10 is that in all age groups proportionately more banded males than females were recovered breeding. This difference is not due to a sampling bias, but to larger numbers of females surviving, thus creating an unequal sex ratio. Because of this some females are unable to obtain a partner and may not breed until they are

TABLE 21. The age of male and female gulls forming a new pair bond after changing mates

Age of females (years)	Age of male (years)										Mean of male
	2	3	4	5	6	7	8	9	10	Unknown	
2											
3		1									3.0
4		1	1							1	3.5
5										3	
6		1		1						4	4.0
7		2								1	3.0
8		1								2	3.0
9		1		1	2	1					4.5
10		2									3.0
Unknown		5	2	2	2		1	2		12	
Mean of female		7.1	4.0	7.5	9.0	9.0					

Note. Percentage with partners with age difference of no more than one year = 26.7%

Percentage with the male being older = 0.0%

Percentage with the female being older = 86.7%

six or seven years old. This is interesting, because in other breeding studies of known aged birds (for example, Yellow-eyed Penguin, *Megadyptes antipodes*, Richdale, 1957; Kittiwake Gull, *Rissa tridactyla*, Coulson, 1966; Starling *Sturnus vulgaris*, Kluijver, 1935; and the Gannet, *Sula bassana*, Nelson, 1966b; Short-tailed Shearwater, *Puffinus tenuirostris*, Serventy, 1967) females breed at an earlier age than males.

5.5 Age of breeding partners

Table 20 gives details of 212 known age pairs. Many partners were of similar age; 68.4% had mates with an age difference of no more than one year and 25.9% of these had partners of the same age. Similar figures have been found for the Yellow-eyed Penguin *Megadyptes antipodes* (Richdale, 1949) and the Kittiwake Gull *Rissa tridactyla* (Coulson, 1966). In 57.1% of all pairs the female was the elder partner. The tendency to mate with a partner of the same or similar age results from the retention of pair bonds and the difference in the timing of the onset of breeding by different aged birds. Because 82.8% of pair bonds are retained, the majority of unmated gulls are birds which have not bred and they are, therefore, likely to breed together. Because males tend to breed at an earlier age than females, there is a discrepancy in the age of partners which is retained from season to season with the retention of pair bonds. Furthermore, the difference in the timing of the onset of breeding in different aged birds means that older gulls changing mates have an increased opportunity of mating with a similar aged gull (Table 21).

TABLE 22. Retention and change of breeding partners

(a) MALES

Age of males	No. changed mates	% changed mates	No. retained mates	% retained mates
2 years	0	-	0	-
3 years	0	-	0	-
4 years	0	-	2	100.0%
5 years	3	33.3%	6	66.6%
6 years	5	35.7%	9	64.3%
7 years	2	13.3%	13	86.7%
8 years	3	17.6%	14	82.4%
9 years	3	18.8%	13	81.2%
10 years	1	50.0%	1	50.0%
Unknown	7	9.5%	67	90.5%
Total	24	16.1%	125	83.9%

(b) FEMALES

Age of males	No. changed mates	% changed mates	No. retained mates	% retained mates
2 years	0	-	0	-
3 years	8	61.5%	5	38.5%
4 years	3	25.0%	9	75.0%
5 years	3	18.8%	13	81.2%
6 years	2	15.4%	11	84.6%
7 years	0	-	16	100.0%
8 years	1	5.3%	18	94.7%
9 years	2	8.7%	21	91.3%
10 years	0	-	2	100.0%
Unknown	9	23.1%	30	76.9%
Total	28	18.3%	125	81.7%

5.6 Retention and change of breeding partners

There is a marked tendency for Red-billed Gulls to retain the partner of the previous breeding season (Table 22). Comparable figures for the maintenance of pair bonds have been recorded in other sea-birds (namely, 94.7% by Laysan Albatross *Diomedea immutabilis* (Rice & Kenyon, 1962); 59% by Yellow-eyed Penguins *Megadyptes antipodes* (Richdale, 1949); 64% by Kittiwake Gulls *Rissa tridactyla* (Coulson, 1966)). There is a marked tendency for older gulls to retain partners. This has also been noted by Coulson for the Kittiwake Gull. It is known that at least 4% of the gulls changed partners because the previous mate had died, but the actual figure may be considerably higher since 66% of the former mates had not been located by October 1969. Twenty-seven per cent of the gulls which changed mates had the former partner breeding on the colony.

Fifty-three per cent of the gulls which changed mates selected partners that were three or four years old (Table 23).

TABLE 23. Ages of gulls breeding with gulls which have changed mates

Sex of new partner	Age of new partner (years)									Unknown age	Total
	2	3	4	5	6	7	8	9	10		
Male	-	6	-	1	2	1	-	-	-	14	24
Female	-	1	3	-	1	1	-	2	1	19	28
Total	-	7	3	1	3	2	-	2	1	33	52

Most were probably inexperienced breeders, as only one was seen breeding in the previous season. Six of the nine new partners over four years of age had bred previously.

5.7 Date of egg laying

In the seasons from 1965-66 to 1968-69, the first clutch was laid by 11 October. The laying period, excluding replacement clutches, lasted from 11 October to 24 December (74 days) in the 1965-66 season; from 9 October to 22 December (74 days) in 1967-68 and from 1 October to 27 December (87 days) in 1968-69. Figure 11 shows the percentage laying at different study areas for the two years, 1967-68 and 1968-69. Despite the long egg laying period, there was a marked synchrony of laying. In each season, peak laying occurred at the same time in most of the study areas, and between the seasons the peak varied only slightly, being earlier in the 1968-69 season.

Table 24 presents the median and mean laying dates in

TABLE 24. Mean and median laying dates of study areas in the 1967-68 and 1968-69 breeding season

Colony	Area	Year	No. nests	Median	Mean	S.D.
Lighthouse	A	1967-68	179	31 Oct.	2 Nov.	15.3 Days
		1968-69	159	5 Nov.	7 Nov.	19.7 Days
Iceplant	A	1967-68	52	6 Nov.	8 Nov.	14.3 Days
		1968-69	108	31 Oct.	3 Nov.	15.6 Days
Rhinohorns	A	1967-68	146	30 Oct.	1 Nov.	12.4 Days
		1968-69	113	28 Oct.	31 Oct.	16.4 Days

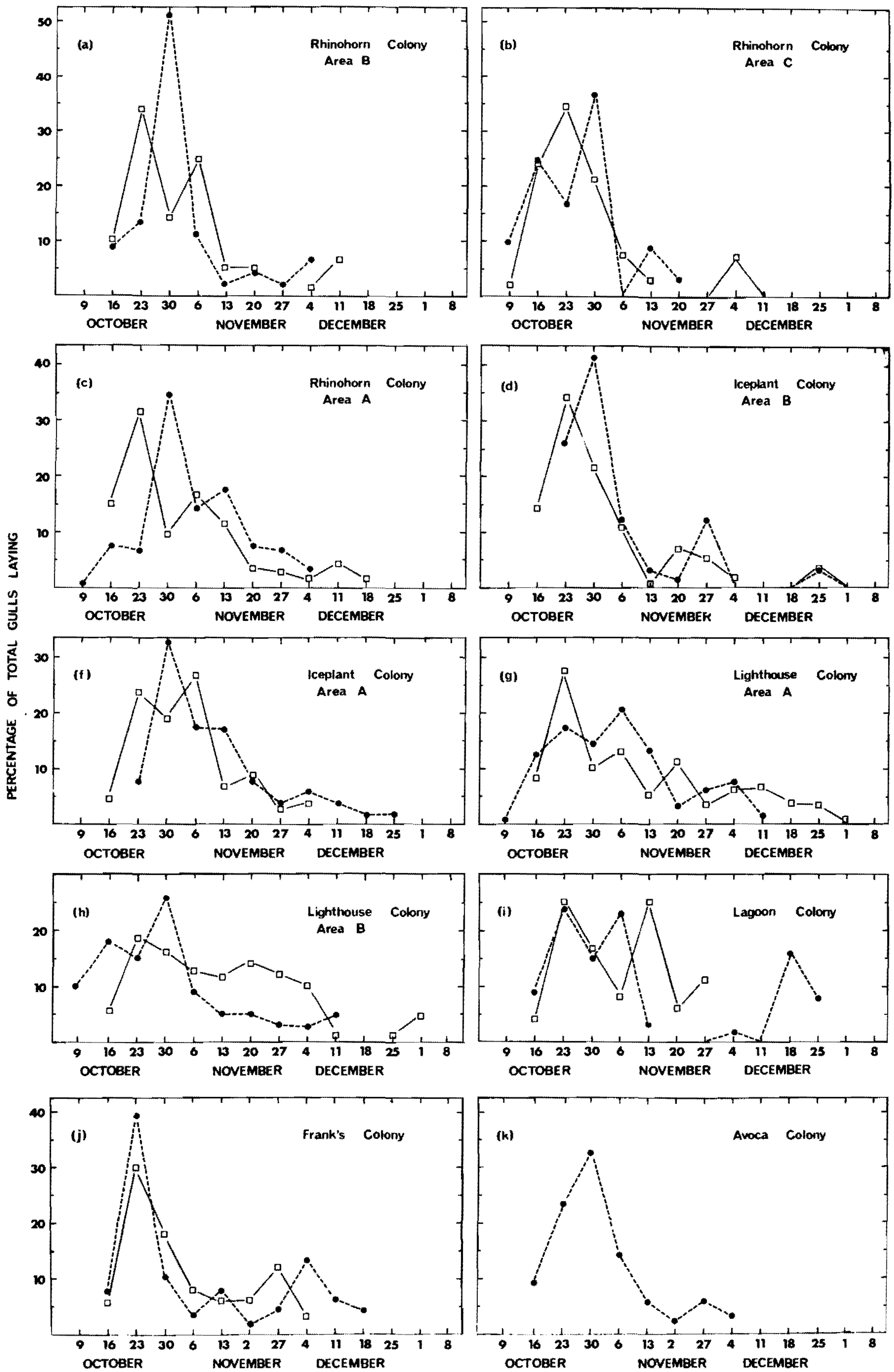

(a) Rhinohorn Colony Area B
(b) Rhinohorn Colony Area C
(c) Rhinohorn Colony Area A
(d) Iceplant Colony Area B
(f) Iceplant Colony Area A
(g) Lighthouse Colony Area A
(h) Lighthouse Colony Area B
(i) Lagoon Colony
(j) Frank's Colony
(k) Avoca Colony
PERCENTAGE OF TOTAL GULLS LAYING
OCTOBER
NOVEMBER
DECEMBER

FIGURE 11. The distribution of egg laying in ten
(a) - (k). study areas in 1967-68 and 1968-69.

study areas where daily checks of nests were made. The dates are remarkably consistent regardless of year or study area. A similar consistency has been recorded for the Gannet, Sula bassana (Nelson, 1966a).

Greater synchrony appears in areas of high elevation (Figure 11 b, d, f) than in lower lying areas (Figure 11 c, g, h). This is to be expected as the higher colonies are preferred sites and attract breeders earlier.

5.8 Incubation

The incubation period varied between 21 and 27 days. In two-egg clutches there was an interval of a day between hatching, but in three-egg clutches there was a difference of two days between the second and third hatchings. Tasker (1970) has shown that males and females spend approximately equal amounts of time in the vicinity of the nest during the incubation period.

In some nests the only contents were shells or stones the sixe of an egg. Some gulls tried to incubate such objects for eight weeks or longer.

5.9 Clutch size

The normal clutch size is two eggs, but a few gulls lay one, three, four and five eggs. The Red-billed Gull is a determinate layer. Removal of one or two eggs during egg laying is not compensated by any further egg production. As in a number of gull species (Weidmann, 1956; Paludan, 1951), the placing of eggs in the nest before laying starts, suppresses the laying of eggs.

The frequency distribution of clutch sizes from marked nests for the four seasons is shown in Table 25. The annual frequencies of clutch size differed significantly among years,

TABLE 25. Frequency distribution of clutch sizes

Clutch size	Breeding Season 1964-65	1965-66	1967-68	1968-69	Total
1	102	116	124	102	444
2	451	553	794	734	2532
3	50	55	101	77	283
4	1	6	1		8
5				1	1
Total	604	730	1020	914	3268
Mean	1.92	1.93	1.98	1.98	1.96
S.D.	0.50	0.51	0.47	0.45	0.48

Note. G statistic for the entire set = 32.35, d.f. = 12, p = < 0.005

however the clutch sizes of individual females in successive seasons (1967-68 and 1968-69) showed no significant difference (Table 26).

Over 72% of the females laid a clutch of the same size in successive seasons; this consistency is also characteristic of the Common Swift *Apus apus* (Lack & Lack, 1951), Alpine Swift *Apus melba*, (Lack & Arn, 1947), Starling *Sturnus vulgaris* (Lack, 1948), Great Tit *Parus major* (Kluijver, 1951), Kittiwake Gull *Rissa tridactyla* (Coulson & White, 1961) and Skylark *Alauda arvensis* (Delius, 1965).

TABLE 26. Clutch size of individual females in 1967-68 and 1968-69

Clutch size 1967	Clutch size 1968						
	1	2	3	Total	% less	% same	% more
1	6	16	1	23	-	26.1%	73.9%
2	15	126	7	148	10.2%	85.1%	4.7%
3	2	12	9	23	60.9%	39.1%	-
	23	154	17	194	14.9%	72.7%	12.4%

Note. Mean clutch size 1967-68 2.00 ± 0.49
Mean clutch size 1968-69 1.97 ± 0.45
$t = 0.0196$, d.f. = 386, $p = > 0.9$

Lack (1948) suggested that the consistency indicated a genetical difference between individuals but Kluijver (1951) believed it resulted from the fact that females living in the same area encountered consistent conditions from year to year.

5.10 Breeding success

The reproductive success in the four seasons studied is summarised in Table 27. There was no significant difference in hatching or fledging success between the 1967-68 and 1968-69 seasons, but that of 1965-66 was significantly smaller. This was because the main study area was in an atypical nesting colony with half being situated on the mainland and half on rocks separated from the mainland by a narrow channel of water. Consequently, the colony was easily entered by Stoats, *Mustela erminea*, and predation was high. Chick mortality did

TABLE 27. Hatching and fledging success

Year	nests	Eggs laid	Eggs hatched	% hatched	Young fledged	% fledged	% fledged that hatch	Mean no. of chicks/ nest
1965 -66	705	1316	714	54.3	525	39.9	73.5	0.74
1967 -68	864	1623	1037	63.9	837	51.6	80.7	0.97
1968 -69	846	1626	988	60.8	817	50.3	82.7	0.97

Note. X^2 (1965-66, 1967-68, 1968-69; % fledged) = 45.873, d.f. = 2, p = <0.005

X^2 (1965-66, 1967-68, 1968-69; % hatched) = 28.794, d.f. = 2, p = <0.005

X^2 (1967-68, 1968-69; % fledged) = 0.5689, d.f. = 1, p = 0.5 - 0.75

not differ seasonally.

The most common cause of egg mortality is predation by Red-billed Gulls and Stoats (in that order). Other potential predators include Black-backed Gulls, Larus dominicanus, Hedgehogs, Erinaceus europaeus and Harrier Hawks, Circus approximans.

The term "failure to hatch" refers to eggs that remain in the nest and do not hatch, including eggs with no sign of embryo development and embryos which have died. These are grouped because it is difficult to distinguish between infertile eggs and those with embryos which died at an early stage.

A large part of egg mortality occurred through the loss of the entire clutch due to predation and swamping of nests (Table 28). Predation usually results in loss of the complete

TABLE 28. Fate of part or whole clutches of eggs

Year	No. of clutches	Category of clutch failing	% of total clutches laid	No. pre-dated	% pre-dated	No. swamped	% swamped
1967 -68	191	whole	22.1%	88	46.1%	89	46.6%
	91	partial	10.5%	18	19.8%	1	1.1%
	72	uncom-pleted	8.3%	32	44.4%	40	55.6%
1968 -69	231	whole	27.3%	112	48.5%	104	45.0%
	74	partial	8.8%	19	25.7%	2	2.7%
	55	uncom-pleted	6.6%	33	60.0%	21	38.2%

clutch. Only 19.8% in 1967-68, and 35.7% in 1968-69 of predated nests had only part of the clutch taken.

When part of the clutch is lost, eggs are not laid to make up the deficiency, but if the complete clutch is lost a replacement clutch is sometimes laid.

An analysis of the breeding success of 112 female gulls in successive seasons revealed that only 8.9% of the gulls failed to raise any chicks to fledging, and 58.9% managed to fledge at least one chick in both seasons.

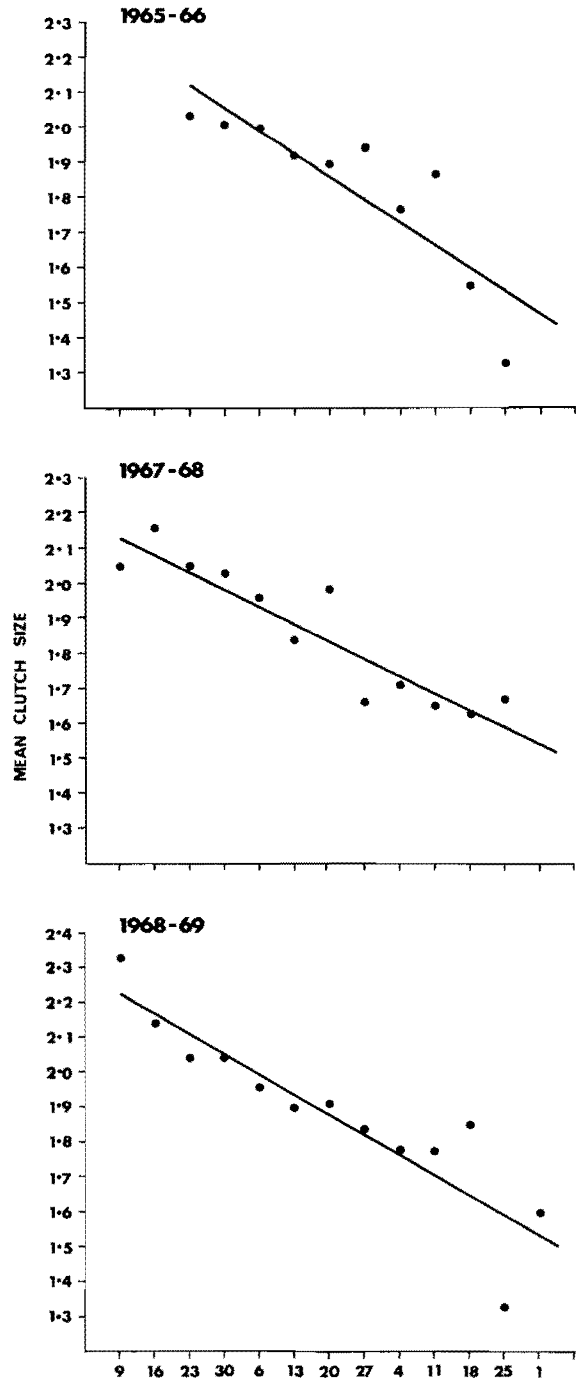

1965-66
1967-68
1968-69
MEAN CLUTCH SIZE
2·4
2·3
2·2
2·1
2·0
1·9
1·8
1·7
1·6
1·5
1·4
1·3
9 16 23 30 6 13 20 27 4 11 18 25 1
OCTOBER
NOVEMBER
DECEMBER

FIGURE 12. Seasonal variation in clutch size.

Regression lines:

1965-66, $y = 2.194 + -0.065x$;

1967-68, $y = 2.187 + -0.057x$;

1968-69, $y = 2.283 + -0.049x$.

6. FACTORS AFFECTING THE BREEDING BIOLOGY

This section examines the factors which affect the breeding biology, in particular the clutch size and chick survival. Many factors interact but at this stage selected factors are treated separately. Post-fledging survival estimates refer to the survival from hatching to the 1 April following banding.

6.1 The influence of laying date

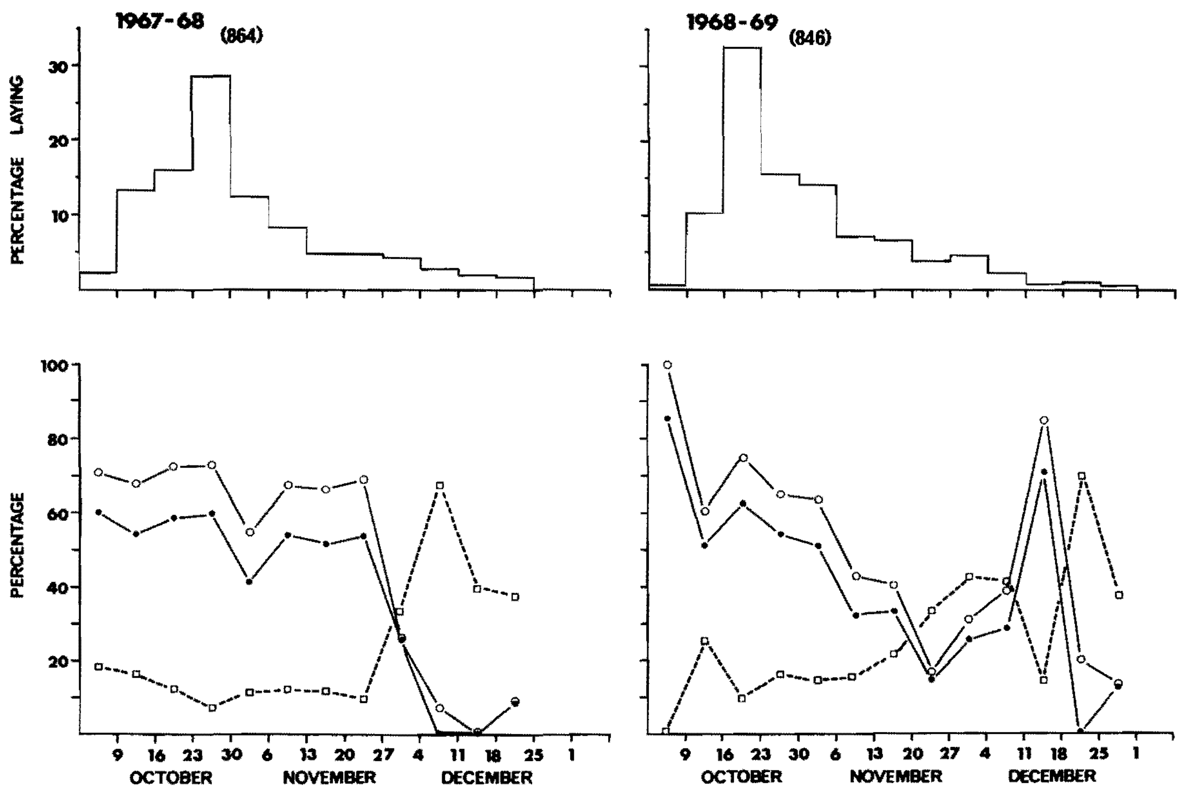
The date egg laying begins has a profound effect on the breeding biology. It influences clutch size, fledging success and post-fledging survival. This section establishes the basic pattern while specific factors affecting the laying date will be examined later.

6.1.(i) Clutch size

The mean clutch size decreases as the season progresses (Figure 12). A regression analysis shows that the mean clutch size decreased by 0.06 eggs in 1965-66, 0.05 eggs in 1967-68 and 0.06 eggs in 1968-69 for each seven day interval after egg laying began.

In each season two egg clutches retained a similar frequency throughout the egg laying period, decreasing only in the latter part of the season (Appendix 4). Clutches of three, four and five eggs occurred mainly in the first half of the egg laying period, whereas single egg clutches became common as the season progressed.

Lack (1966) believes that the seasonal decline in clutch size is an adaptive response to the availability of food when



1967-68
(864)
1968-69
(846)
PERCENTAGE LAYING
30
20
10
PERCENTAGE
100
80
60
40
20
9 16 23 30 6 13 20 27 4 11 18 25 1
OCTOBER
NOVEMBER
DECEMBER

FIGURE 13. Changes in hatching success, predation rate of eggs and breeding success of Red-billed Gulls with laying date, compared with the distribution of egg laying. (O - O - O hatching success, ● - ● - ● breeding success, □ -- □ -- □ predation rate of eggs).
(Kendall Rank Correlation Coefficient $\tau = +0.53$, $p = 0.025 - 0.01$ in 1967-68, and $\tau = +0.47$, $p = 0.05 - 0.025$ in 1968-69.)

nestlings are present. Perrins (1965), however, argues that there is no evidence that birds can predict the level of prey populations, and believes that Great Tits Parus major adjust their clutches by other factors such as the appearance of the habitat. In the Red-billed Gull it seems more likely that the conditions prevailing immediately prior to laying determine clutch size. These factors will be discussed later.

6.1.(ii) Breeding success

There is a marked decline in reproductive success as the season progresses (Figure 13). The major cause is increase in egg predation.

The hatching success in 1967-68 remained relatively constant for clutches laid until the 27 November but in 1968-69, apart from fluctuations in the latter part of the season, the proportion hatched declined as the season progressed. The proportion of chicks fledged paralleled the percentage hatched throughout both seasons which suggests that the parents are able to find enough food for the young.

Patterson (1965) has shown a relationship in the Black-headed Gull Larus ridibundus between the number of gulls laying at a given period and the subsequent breeding success. Predation was the main mortality agent of nestlings and eggs at the colony studied by Patterson and he postulated that synchronization of laying served an antipredator function by concentrating nesting into the shortest possible time, thus reducing the total losses over the season. In the Red-billed Gull evidence for this relationship is conflicting. If the study areas are grouped there is a correlation (Figure 13), but if treated separately only six of the twenty areas studied since 1965-66 show a positive correlation (Appendix 5). It is probably a coincidence that some of the areas show a posi-

TABLE 29. Survival of young in relation to the date of hatching

Date	1965-66 season		1967-68 season		1968-69 season	
	No. banded	No. recovered	No. banded	No. recovered	No. banded	No. recovered
17-23 Oct.					2	
24-30 Oct.			3	0	2	0
31- 6 Nov.	51	5 (9.8%)	26	6 (23.1%)	17	2 (11.8%)
7-13 Nov.	185	33 (17.8%)	133	22 (16.5%)	526	63 (12.0%)
14-20 Nov.	160	32 (20.0%)	345	53 (15.4%)	394	34 (8.6%)
21-27 Nov.	192	10 (5.2%)	255	38 (14.9%)	371	16 (4.3%)
28- 4 Dec.	163	7 (4.3%)	102	7 (6.9%)	194	7 (3.6%)
5-11 Dec.	73	2 (2.7%)	78	6 (7.7%)	255	11 (4.3%)
12-18 Dec.	47	3 (6.4%)	101	9 (8.9%)	183	2 (1.1%)
19-25 Dec.	19	2 (10.0%)	31	0	67	1 (1.5%)
26- 1 Jan.			166	19 (11.4%)	157	9 (5.7%)
2- 8 Jan.					45	0
9-15 Jan.					46	0
16-22 Jan.					15	0

tive correlation since the high predation of chicks and eggs from clutches laid late in the season happens to coincide with small numbers of clutches being laid. The most probable causes of greater predation late in the season are more active searching by predators or a change in the parental behaviour which makes eggs easier to obtain (Brown, 1967a). These factors will be discussed further later. The colony most likely to exhibit a valid correlation was the Sugarloaf Colony in 1965-66. Large numbers of chicks and eggs were taken by Stoats *Mustela erminea* and noticeably more chicks were fledged from clutches that were laid at the peak laying period. Furthermore this colony has a high coefficient (τ = +0.65, $p = < 0.005$).

6.1.(iii) Post-fledging survival

Table 29 gives the survival rates of young Red-billed gulls which were known to be alive at 1 April following banding ($2\frac{1}{2}$ - 4 months of age). All chicks were banded less than four days after hatching. The majority of recoveries were made by sight, using 7 x 30 field glasses. By offering food, the gulls can be attracted close enough for band numbers to be read.

In all seasons of study, gulls hatched early have a greater chance of survival than those hatched later. This has also been observed in the Great Tit *Parus major* (Perrins, 1965) and the Manx Shearwater *Puffinus puffinus* (Perrins, 1966).

The survival figures for the 1965-66 season are not comparable with those obtained for 1967-68 and 1968-69 as no attempt was made to recover banded gulls in 1966-67 until the 1967-68 breeding season. The estimate of survival thus refers to gulls recovered after the second year of life. The survival rates for the 1967-68 cohort include recoveries made

TABLE 30. Influence of female age on the date of egg laying

Age of female	1967-68 No. females considered	Mean laying date	S.D.	1968-69 No. females considered	Mean laying date	S.D.
2 years	3	20 Nov.	7.4	-	-	-
3 years	19	17 Nov.	10.4	13	21 Nov.	15.2
4 years	25	11 Nov.	14.7	30	19 Nov.	15.2
5 years	42	8 Nov.	15.3	24	4 Nov.	18.3
6 years	33	2 Nov.	13.8	49	7 Nov.	16.0
7 years	54	31 Oct.	14.4	42	5 Nov.	16.4
8 years	32	30 Oct.	10.3	44	31 Oct.	17.0
9 years	6	7 Nov.	11.0	31	31 Oct.	16.0
10 years	-			5	27 Oct.	5.3

Note.

t(2-3 yrs)(1967-68) = 0.4746, d.f. = 20, p = > 0.50

t(3-4 yrs)(1967-68) = 1.4902, d.f. = 42, p = 0.2-0.1

(1968-69) = 0.3961, d.f. = 41, p = > 0.5

t(3-5 yrs)(1967-68) = 2.3269, d.f. = 59, p = 0.025-0.010

(1968-69) = 2.8694, d.f. = 35, p = 0.01-0.005

t(5-8 yrs)(1967-68) = 2.5572, d.f. = 72, p = 0.025-0.010

(1968-69) = 0.9044, d.f. = 66, p = 0.50-0.40

t(6-8 yrs)(1967-68) = 1.7111, d.f. = 63, p = 0.10-0.05

(1968-69) = 2.0498, d.f. = 91, p = 0.05-0.025

t(4-5 yrs)(1967-68) = 0.7897, d.f. = 65, p = 0.50-0.40

(1968-69) = 3.2892, d.f. = 52, p = 0.005-0.001

in 1968 and 1969, but those for 1968-69 are based on recoveries made only in 1969.

6.2 The influence of female age

6.2.(i) Date of laying

The effects of female age on the time of egg laying is shown in Table 30. Female gulls tend to lay earlier with increasing age. In both seasons there is no statistical difference in the mean laying dates of two and three year old females, or between three and four year olds, but the differences are significant between three and five year old females. It is probable that many of the three and four year old females are breeding for the first time. The data for 1967-68 show that five and six year old females laid significantly later than did eight year olds, while in 1968-69 five year old females laid significantly earlier than four year olds, and eight year old females laid significantly earlier than six year olds.

The differences in the mean laying dates between the age classes are large. In other species where a difference in laying date has been shown between old and young birds the difference is usually only a few days, e.g. Starling *Sturnus vulgaris* (Kluijver, 1933), Song Sparrow *Melospiza melodia* (Nice, 1937), Cormorant *Phalacrocorax carbo* (Kortlandt, 1942), Common Tern *Sterna hirundo* (Austin, 1945), Great Tit *Parus major* (Kluijver, 1951; Perrins, 1965), Kittiwake Gull *Rissa tridactyla* (Coulson & White, 1956, 1960), Storm Petrel *Hydrobates pelagicus* (Davis, 1957), Blackbird *Turdus merula* (Snow, 1958) and the Pied Flycatcher *Ficedula hypoleuca* (v Haartman, 1967).

TABLE 32. The clutch size of young (2 - 4 years) and old (6 - 10 years) females according to the date of laying

Date of laying	Young Females			Old Females			Difference of means (p)
	No. of clutches	Mean clutch	S.D.	No. of clutches	Mean clutch	S.D.	
3- 9 Oct.	1	2.00		1	2.00		
10-16				23	1.91	0.42	
17-23				58	2.03	0.42	
24-30	10	1.70	0.48	73	1.95	0.44	0.1
31- 6 Nov.	8	1.63	0.74	53	1.96	0.34	0.05-0.025
7-13	14	1.64	0.50	27	1.93	0.47	0.20-0.10
14-20	5	1.80	0.45	18	2.06	0.54	0.40-0.20
21-27	15	1.53	0.52	9	1.78	0.67	0.40-0.20
28- 4 Dec.	15	1.53	0.52	10	1.90	0.32	0.05
5-11	6	1.33	0.52	7	1.71	0.49	0.20
12-18				5	1.80	0.45	
19-25	3	1.33		2	1.00		
26- 1 Jan.				1	1.00		

6.2.(ii) Clutch size

The clutch sizes of females of known age in all years of study are shown in Table 31. Statistically there is no difference between the mean clutches of two and three year old females or between three and four year old females, but the differences are highly significant between three and five year olds and also between four and five year olds. There

TABLE 31. Influence of age on clutch size

Age of female	No. in sample	Clutch size 1	2	3	4	Mean clutch	S.D.	Percent composition 1	2	3	4
2 years	9	6	3			1.33	0.50	66.7%	33.3%		
3 years	64	23	38	3		1.69	0.56	35.9%	59.4%	4.7%	
4 years	92	26	63	2	1	1.76	0.54	28.3%	68.5%	2.2%	1.1%
5 years	106	10	84	10	2	2.09	0.52	9.4%	79.3%	9.4%	1.9%
6 years	122	14	99	8	1	1.98	0.46	11.5%	81.1%	6.6%	0.8%
7 years	104	10	83	10	1	2.08	0.48	9.6%	79.8%	9.6%	1.0%
8 years	75	11	60	4		1.93	0.44	14.7%	80.0%	5.3%	
9 years	37	2	33	2		2.00	0.33	5.4%	89.2%	5.4%	
10 years	5	3	2			1.40	0.54	60.0%	40.0%		

t(2 - 3 years) = 1.8280, d.f. = 71, p = 0.1 - 0.5
t(3 - 4 years) = 0.7844, d.f. = 154, p = 0.4
t(3 - 5 years) = 4.0637, d.f. = 168, p = < 0.001
t(4 - 5 years) = 3.8280, d.f. = 196, p = < 0.001
t(5 - 9 years) = 0.7987, d.f. = 141, p = 0.4

is no significant increase in clutch size with further increase in age after the fifth year. It has been demonstrated for a

TABLE 33. Breeding success of known age females

	Age of female (years)								
	2	3	4	5	6	7	8	9	10
No. clutches	6	45	76	86	90	78	64	31	4
No. eggs	8	72	129	170	175	161	121	62	6
No. hatched	6	49	82	110	131	110	93	33	5
% hatched	75.0%	68.1%	63.6%	64.7%	74.9%	68.3%	76.9%	53.2%	83.3%
No. fledged	3	39	65	100	102	80	78	25	5
% fledged	37.5%	54.2%	50.4%	58.8%	58.3%	49.7%	64.5%	40.3%	83.3%
% fledged that hatch	50.0%	79.6%	79.3%	90.9%	77.9%	72.7%	83.9%	75.8%	100.0%
No. fledged per pair	0.50	0.87	0.86	1.16	1.13	1.03	1.22	0.81	1.25

Note. χ^2 (all age groups, % hatched) = 17.462, d.f. = 8, p = 0.025
χ^2 (all age groups, % fledged) = 17.689, d.f. = 8, p = 0.025

large number of bird species, that young females lay smaller clutches than older birds, e.g. several species listed by Lack (1947), Yellow-eyed Penguin Megadyptes antipodes (Richdale, 1949), Great Tit (Kluijver, 1951; Perrins, 1965), and the Kittiwake Gull (Coulson & White, 1961).

The percentage occurrence of single egg clutches is highest in two year old females, and tends to decrease with age. The proportions of two egg clutches laid remained relatively constant for gulls over four years of age. Three and four egg clutches were not laid by two year old females.

In Table 32 the data for the 1967-68 and 1968-69 seasons are combined to show the relationship between the date of egg laying and the clutch size of young (2 - 4 years) and old females (6 - 10 years). There is a tendency for young females to lay smaller clutches than older females laying at the same time. The differences are statistically significant in two of the weeks (31 October - 6 November and 28 November - 4 December).

6.2.(iii) Breeding success

The influence of the female's age on breeding success in all years of study is shown in Table 33. The hatching and fledging success of different aged birds shows a significant deviation from independence, but there is no marked tendency for increasing hatching or fledging success with an increase in age. There is, however, a progressive increase in the number of chicks fledged per pair up to the fifth year, due to older gulls laying larger clutches and therefore raising more chicks per pair.

Table 34 shows the egg losses by predation of known aged gulls. The age of the male, but not the female, is closely correlated with the number of eggs lost by predation. This

TABLE 34. Predation rate on clutches of known aged gulls

(a) FEMALES

Age of female	No. of nests	No. of eggs	Eggs predated	Per cent predated
2 years	6	8	1	12.5%
3 years	45	72	13	18.1%
4 years	76	129	35	27.1%
5 years	86	170	35	20.6%
6 years	90	175	27	15.4%
7 years	78	161	24	14.9%
8 years	64	121	13	8.1%
9 years	31	62	14	22.6%
10 years	4	6	0	0 %

Note. Kendall rank correlation + 0.0278, p = 0.10

(b) MALES

Age of male	No. of nests	No. of eggs	Eggs predated	Per cent predated
2 years	38	60	13	21.7%
3 years	106	189	56	29.6%
4 years	86	167	33	19.8%
5 years	127	247	32	13.0%
6 years	134	270	34	12.6%
7 years	104	215	32	14.9%
8 years	79	164	18	11.0%
9 years	52	100	5	5.0%
10 years	8	16	2	12.5%

Note. Kendall rank correlation + 0.7222, p = 0.005

TABLE 35. Breeding success of different aged females according to the date of egg laying

Date	2 - 4 year females					5 - 10 year females				
	No. nests	No. eggs	No. fledged	% fledged	No. fledged per pair	No. nests	No. eggs	No. fledged	% fledged	No. fledged per pair
3- 9 Oct.	1	2	2	100.0%		1	2	0	0.0%	
10-16	-	-	-	-		19	38	18	47.4	
17-23	1	2	1	50.0	58.5%	52	105	68	64.8	54.0%
24-30	9	16	11	68.8	1.0 fledged/ pair	60	117	64	54.7	1.08 fledged/pair
31- 6 Nov.	13	21	10	47.6		43	88	39	44.3	
7-13	13	21	9	42.9		19	36	20	55.6	
14-20	3	6	2	33.3		16	32	12	37.5	
21-27	13	18	1	61.1		9	16	9	56.3	
28- 4 Dec.	14	21	2	9.5	36.0%	7	13	2	15.4	45.0%
5-11	3	4	3	75.0	0.75 fledged/pair	3	6	2	33.3	0.85 fledged/pair
12-18	1	2	0	0.0		3	6	4	66.7	
19-25	2	3	0	0.0		1	1	0	0.0	
26- 1 Jan.						1	1	1	100.0	
Total	73	116	51	44.0	0.70	234	461	239	51.8	1.02

Note. X^2 (% fledged, 3 Oct. - 6 Nov.) = 0.3045, d.f. = 1, p = 0.75 - 0.5
X^2 (% fledged, 7 Nov. - 1 Jan.) = 1.5089, d.f. = 1, p = 0.25 - 0.10
X^2 (% fledged, 2 - 4, 5 - 10) = 1.9856, d.f. = 1, p = 0.25 - 0.10

is because nest sites are selected by the males and normally the older males obtain the most secure territories, the younger taking up more vulnerable nest territories later in the season.

The effects of the female's age and the date of egg laying on the breeding success are shown in Table 35. There is no significant difference in the breeding success between young and old females commencing laying at the same time. Young and old females are equally successful at raising eggs to fledged young at the same time in the breeding season: the lower overall breeding success of the 2 - 4 year cohort is because more of them commence breeding after the median laying date (67.1% for 2 - 4 year olds, c.f. 25.2% for the gulls 5 - 10 years) at a time when a lower breeding success is general.

Table 36 shows the influence of age on fertility among 482 females of known age. "Infertile eggs" include eggs

TABLE 36. Influence of age on fertility

	Age of female (years)								
	2	3	4	5	6	7	8	9	10
No. clutches	6	44	76	88	91	78	64	31	4
No. eggs	8	71	129	175	178	161	121	62	6
No. "infertile"	1	2	4	7	3	8	3	-	1
%"infertile"	12.5%	2.8%	3.1%	4.0%	1.7%	5.0%	2.5%	0.0%	16.7%

unfertilized and eggs which contain dead embryos. The data show there is no apparent relation between fertility and age. However there are indications that the situation might be

TABLE 37. Post-fledging survival of young Red-billed Gulls from female parents of known age

Female parent	1965-66 No. chicks banded	1965-66 Chicks recovered	1967-68 No. chicks banded	1967-68 Chicks recovered	1968-69 No. chicks banded	1968-69 Chicks recovered	Total No. chicks banded	Total Chicks recovered
2 years	4	1 (25.0%)	5	0 (0%)	-	-	9	1 (11.0%)
3 years	28	1 (3.6%)	16	0 (0%)	7	0 (0%)	51	1 (2.0%)
4 years	33	1 (3.0%)	22	5 (22.7%)	14	1 (7.1%)	69	7 (10.1%)
5 years	46	3 (6.5%)	30	4 (13.3%)	24	1 (4.2%)	100	8 (8.0%)
6 years	42	1 (2.4%)	25	4 (16.0%)	51	1 (2.0%)	118	6 (5.1%)
7 years	9	1 (11.1%)	38	4 (10.5%)	46	1 (2.2%)	93	6 (6.5%)
8 years			36	10 (27.8%)	42	0 (0%)	78	10 (12.8%)
9 years			4	1 (25.0%)	25	1 (4.0%)	29	2 (6.9%)
10 years					4	1 (25.0%)	4	1 (25.0%)

found to be different for 2 year olds and 10 year olds.

6.2.(iv) Post-fledging survival

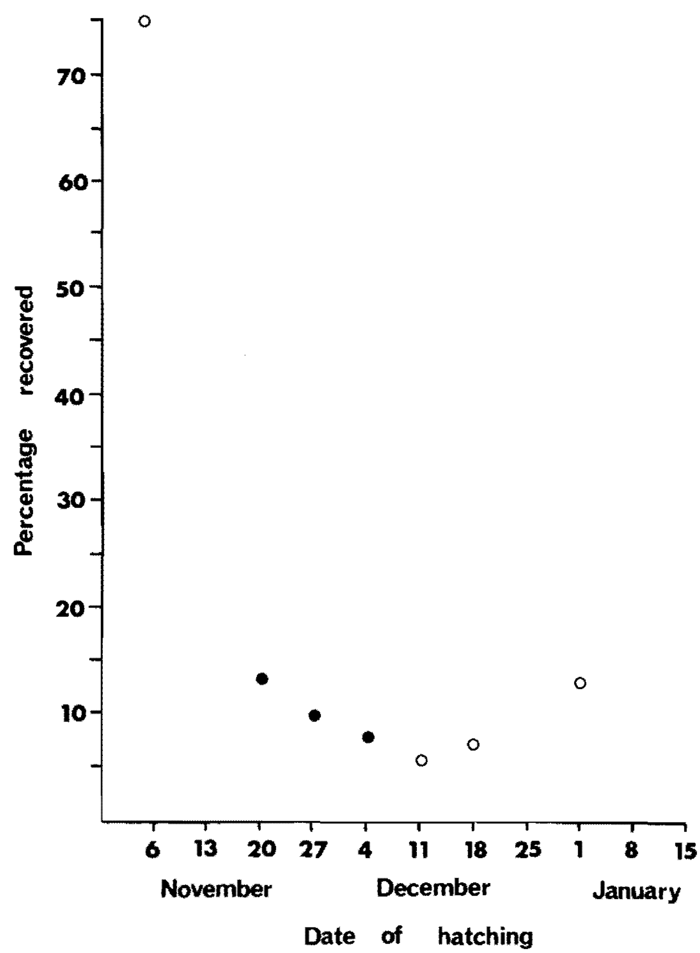
In Table 37 the survival of young gulls is examined in relation to the age of the female parent. Each recovery refers to a gull known to survive after 1 April following banding. Taking into consideration recoveries from all years of study, chicks from 2 - 3 year old females had a lower survival rate (3.3%) than did chicks from older females (8.1%) but the differences are not significant (p = 0.25 - 0.10).

Moreover, the chicks from the 4 - 10 year old females show a marked variation in survival according to the date of hatching (Figure 14). The chance of survival decreases the later in the season the chick hatches. There are insufficient recoveries of chicks of 2 - 3 year old females to assess the survival figures according to the date of hatching. In the Great Tit *Parus major*, Perrins (1970) has similarly shown that survival of young of females of any age diminishes the later the young are hatched. Therefore, the later a bird breeds the less likely it is to produce surviving young, irrespective of the age of the parent.

6.3 The influence of male age

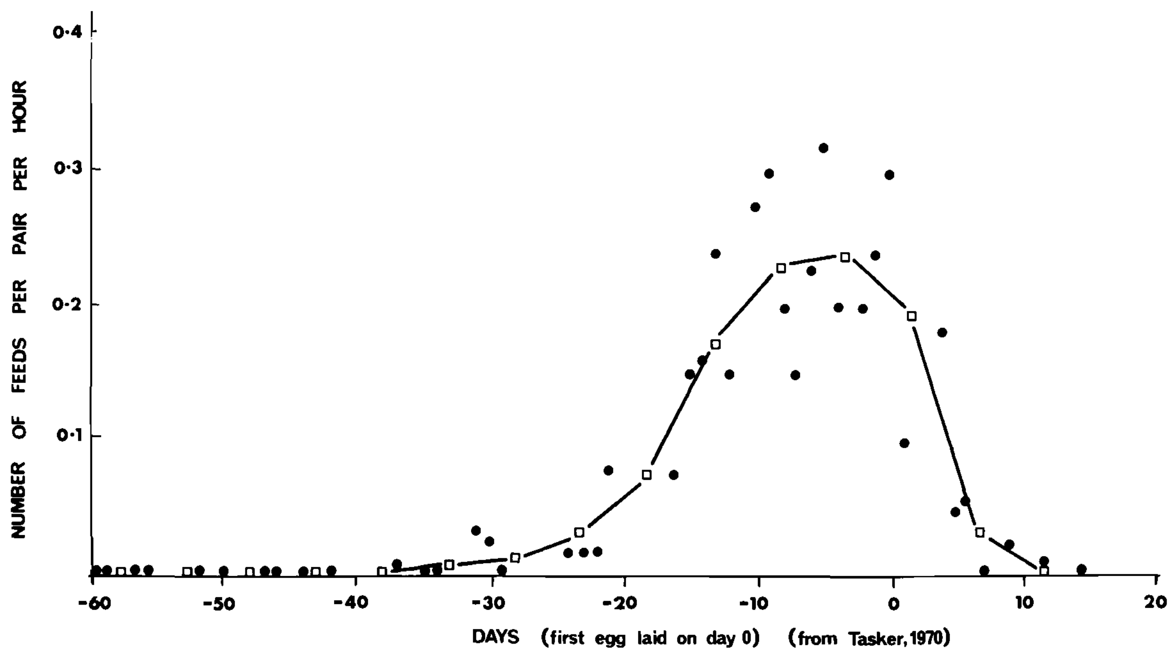
6.3.(i) Courtship feeding

Prior to egg laying and in the early part of the incubation period the male plays a significant role in feeding the female (Plate 2). Tasker (1970) has shown that the number



Percentage recovered
70
60
50
40
30
20
10
6
13
20
27
4
11
18
25
1
8
15
November
December
January
Date of hatching

FIGURE 14. Post-fledging survival of young Red-billed Gulls from females 5 - 10 years of age in relation to the date of hatching. Recoveries were made after 1 April ($2\frac{1}{2}$ - 4 months following banding). Solid circles represent more than five recoveries and open circles are based on fewer than five.



NUMBER OF FEEDS PER PAIR PER HOUR
0·4
0·3
0·2
0·1
-60
-50
-40
-30
-20
-10
0
10
20
DAYS (first egg laid on day 0) (from Tasker, 1970)

FIGURE 15. Changes in the average frequency of "courtship feeding" during the breeding season (□ represents five day averages).

PLATE 2. "Courtship feeding". Male (foreground) regurgitating food for the female. The food consists mainly of planktonic euphausiids Nyctiphanes australis.

of "courtship feeds" per pair per hour increases in frequency about 20 days before egg laying, and a peak exists for about 10 days immediately prior to laying (Figure 15). At the peak of "courtship feeding" the male feeds the female about once every four hours (Tasker, 1970). Thus, throughout the day, the female receives approximately four feeds from the male plus whatever food she is able to obtain for herself. Brown (1967b) believes that courtship feeding, as well as being an essential prelude to successful copulation, has the additional practical advantage of providing the female with extra food at a time when she probably needs it. Similarly, Royama (1966) working with the Great Tit *Parus major* and the Blue Tit *P. caeruleus*, has emphasized the importance of the food received in "courtship feeds", and this has been confirmed by recent work by Krebs (1970) for the Blue Tit.

In the Red-billed Gull the importance of "courtship feeding" can be judged from the knowledge that in the twelve days prior to the laying of the first egg the female spends approximately 85% of her time at the nest territory, whereas males are present only 42% of the time (Table 17).

The food required to form eggs is considerable and much of this has to be collected within a short space of time (Perrins, 1970). Brown (1967b) has shown that the accelerated growth phase of the ovary starts about 10 days before laying in the Lesser Black-backed Gull *Larus fuscus*, and this coincides with the peak in "courtship feeding".

As the male plays a significant role in food collection for the female during the period when extra food is required, the selection of a young or inexperienced male, which is perhaps not proficient at obtaining food, may influence the reproductive biology considerably.

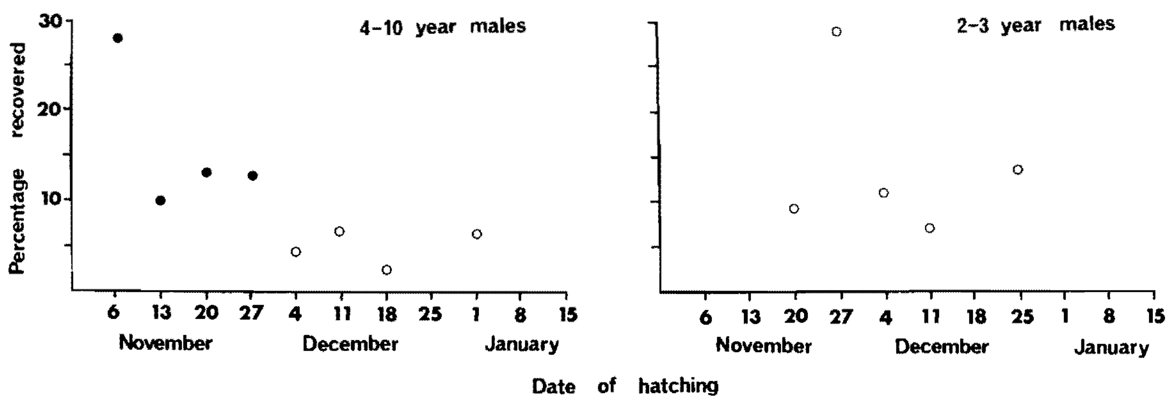

4-10 year males
30
20
10
Percentage recovered
6
13
20
27
4
11
18
25
1
8
15
November
December
January
2-3 year males
6
13
20
27
4
11
18
25
1
8
15
November
December
January
Date of hatching

FIGURE 16. Post-fledging survival of young Red-billed Gulls to 1 April following banding ($2\frac{1}{2}$ - 4 months after banding) in relation to the date of hatching and age of male. Solid circles represent more than five recoveries and open circles are based on fewer than five.

TABLE 38. Laying dates of females five years of age and older breeding with different aged males

Age of male	No. nests	Mean laying date	S.D.
+ 5 years	100	28.5 Oct.	16.1
4 years	18	9.7 Nov.	19.9
3 years	14	10.9 Nov.	19.2
2 years	2	28.0 Nov.	-

Note.

t(+ 5 - 3 years) = 2.8422, d.f. = 112, p = 0.01 - 0.001

t(+ 5 - 4 years) = 2.8682, d.f. = 116, p = 0.01 - 0.001

TABLE 39. Laying dates of females two - four years of age breeding with different aged males

Age of male	No. nests	Mean laying date	S.D.
+ 5 years	7	31.1 Oct.	12.8
4 years	8	13.5 Nov.	18.2
3 years	13	25.6 Nov.	11.6
2 years	10	17.2 Nov.	8.6

Note.

t(+ 5 - 3 years) = 4.5402, d.f. = 18, p = < 0.001

t(+ 5 - 4 years) = 1.6261, d.f. = 13, p = 0.2 - 0.1

t(+ 5 - 2 years) = 3.3170, d.f. = 15, p = 0.01 - 0.001

6.3.(ii) Date of laying

Tables 38 and 39 show the effects of the age of the male in relation to that of the female on the time of laying. In general, females of both age cohorts (2 - 4 and 5 - 10 years) bred earlier in the season with increasing age of the male partner. In addition, 2 - 4 year old females breeding with males over five years of age, laid significantly earlier than females over five years of age breeding with three year old males.

6.3.(iii) Clutch size

The effects of the age of the male on clutch size is shown in Tables 40 and 41. There is a progressive increase in mean clutch size with an increase in the age of the male partner. The difference in mean clutch size of females five years and older breeding with males over five years, and with three year old males, is highly significant. Similarly, the clutch sizes of females two to four years of age breeding with males over five years of age, are statistically larger than clutch sizes laid by these females when they breed with males only three years of age.

6.3.(iv) Post-fledging survival

Table 42 shows that the older males (4 - 10 years) produce more young surviving after 1 April following banding than two and three year old males. As was also found for females, the survival rate varies according to the date of hatching for gulls of the same age cohort (Figure 16).

TABLE 40. Clutch size of females five years of age and older breeding with different aged males

Age of male	No. males	Clutch size 1	2	3	4	Mean	S.D.	Percentage composition 1	2	3	4
+ 5 years	99	7	82	9	1	2.04	0.45	7.1%	82.8%	9.1%	1.0%
4 years	17	2	15	-	-	1.88	0.33	11.8%	88.2%		
3 years	14	6	8	-	-	1.57	0.51	42.9%	57.1%		
2 years	2	1	1	-	-	1.50	0.71	50.0%	50.0%		

t (+ 5 years - 4 years) = 1.3965, d.f. 114, p = 0.2 - 0.1

t (+ 5 years - 3 years) = 4.7625, d.f. 111, p = 0.001

TABLE 41. Clutch size of females 2 - 4 years of age breeding with different aged males

Age of male	No. males	Clutch size 1	2	3	4	Mean	S.D.	Percentage composition 1	2	3	4
+ 5 years	7	1	6	-	-	1.86	0.38	14.3%	85.7%		
4 years	8	3	5	-	-	1.63	0.52	37.5%	62.5%		
3 years	13	5	8	-	-	1.62	0.51	38.5%	61.5%		
2 years	10	6	4	-	-	1.40	0.52	60.0%	40.0%		

t (+ 5 years - 3 years) = 1.0822, d.f. = 18, p = 0.3

t (+ 5 years - 2 years) = 1.9758, d.f. = 15, p = 0.1 - 0.05

TABLE 42. Post-fledging survival of young Red-billed Gulls from male parents of known age

Male parent	1965-66		1967-68		1968-69		Total	
	No. chicks banded	Chicks recovered	No. chicks banded	Chicks recovered	No. chicks banded	Chicks recovered	No. chicks banded	Chicks recovered
2 years	11	1 (9.1%)	22	2 (9.1%)	2	0	35	3 (8.6%)
3 years	43	4 (9.3%)	26	2 (7.7%)	32	1 (3.1%)	101	7 (6.9%)
4 years	33	4 (12.1%)	39	9 (23.1%)	36	3 (8.3%)	108	16 (14.8%)
5 years	66	9 (13.6%)	33	7 (21.2%)	45	2 (4.4%)	144	18 (12.5%)
6 years	59	9 (15.3%)	40	6 (15.0%)	69	2 (2.9%)	168	17 (10.1%)
7 years	24	4 (16.7%)	52	5 (9.7%)	61	2 (3.3%)	137	11 (8.0%)
8 years			44	5 (11.4%)	74	4 (5.4%)	118	9 (7.6%)
9 years			4	1 (25.0%)	80	7 (8.8%)	84	8 (9.5%)
10 years					13	0	13	0

6.4 The influence of retention or change of the pair-bond

6.4.(i) Breeding condition

Table 43 shows the influence of change or retention of a mate on male weights at the start of the incubation period. Female weights have not been considered because these were recorded at various stages during the completion of the clutch. Females which have completed egg laying weigh considerably less than those weighed when the clutch is partially completed. Male weights are not subject to such variations.

TABLE 43. Influence of change or retention of mates on the weight of males at incubation

Status of male	No. males	Mean weight (grams)	S.D.
Retained mate	88	309.6	22.3
Changed mate	24	302.9	14.7

Note. $t = 1.389$, d.f. $= 110$, $p = 0.2 - 0.1$

Males which retain mates tend to be heavier early in the incubation period than those males which change, but the differences are not significant. This phenomenon requires further examination. If the differences are real, the better condition of males retaining mates is probably because

TABLE 44. Influence of change and retention of the pair bond on the date of egg laying

(a) FEMALES

1968 age of female	Pair bond retained: No. females	Mean laying date	S.D.	Pair bond changed: No. females	Mean laying date	S.D.
2 years	-			-		
3 years	-			-		
4 years	2	12.0 Nov.	9.0	-		
5 years	5	27.6 Oct.	12.7	3	1.3 Nov.	11.4
6 years	9	29.6 Oct.	7.9	5	7.0 Nov.	11.5
7 years	12	2.6 Nov.	16.3	2	9.5 Nov.	11.5
8 years	13	24.1 Oct.	8.6	3	29.3 Nov.	22.1
9 years	12	30.7 Oct.	16.6	3	3.0 Nov.	12.0
10 years	1	1.0 Nov.		1	18.0 Nov.	
Unknown	68	26.7 Oct.	12.5	7	5.6 Nov.	10.2
Total	122	28.1 Oct.	13.1	24	7.5 Nov.	15.8

Note. t(changing - retaining mates = 3.4395, d.f. = 144, $p = <0.001$

(b) MALES

1968 age of female	Pair bond retained: No. males	Mean laying date	S.D.	Pair bond changed: No. males	Mean laying date	S.D.
2 years	-			-		
3 years	5	18.4 Nov.	6.3	8	8.0 Nov.	15.0
4 years	9	3.8 Nov.	14.8	3	20.0 Nov.	12.3
5 years	12	23.0 Oct.	6.5	3	4.3 Nov.	17.0
6 years	12	28.2 Oct.	16.9	2	1.5 Nov.	1.5
7 years	14	27.2 Oct.	13.1	-		
8 years	18	23.5 Oct.	7.6	1	7.0 Nov.	
9 years	21	21.6 Oct.	7.7	2	19.5 Nov.	1.5
10 years	2	31.0 Oct.	1.0	-		
Unknown	29	1.1 Nov.	13.5	8	31.7 Oct.	10.3
Total	122	28.1 Oct.	13.1	27	4.8 Nov.	14.2

Note. t(changing - retaining mates = 2.7284, d.f. = 147, $p = 0.01-0.005$

they are able to spend more time feeding than would be possible if they had to defend a territory and attract a mate. This contention is supported by recoveries of colour marked gulls away from Kaikoura in the pre-breeding period. In August and September, at Wellington and Lyttelton Harbours, colour marked gulls have been observed which were known to have bred together in the previous breeding season. This contrasts with the situation in winter when loose pair bonds are not held. Some pair bonds are re-established early in August on the return of the birds to Kaikoura, and the pairs travel up and down the coast searching for plankton swarms where competition is less. Unpaired gulls are not able to do this.

6.4.(ii) Date of laying

Females which retained mates from the previous breeding season bred on average 10.4 days earlier than those which changed mates (Table 44). Similarly, when males changed mates the mean laying date of the new mate was 7.7 days later than if they retained mates. The effects of the retention of breeding partners are similar in the Kittiwake Gull *Rissa tridactyla* (Coulson, 1966). Coulson has said - and this study also shows - that there is considerable variation in laying dates among birds changing mates, but the variability is greatest among birds changing mates. The retention of a mate, Coulson believes, brings about a greater uniformity in the breeding time. Although this may be considered generally true for the Red-billed Gull, 50% of the gulls changing mates bred earlier than they did the previous season, so although there is an advantage in retaining the pair bond, sometimes there is an advantage in breaking it. Coulson has been able to show that gulls retaining mates lay progressively earlier with increased breeding experience. In the Red-billed Gull, samples of the age classes retaining males, especially younger birds, are too small to examine the trend noted by Coulson.

6.4.(iii) Clutch size

Females which retain the pair-bond lay 0.27 eggs per clutch more than those which change mates ($p = 0.01 - 0.05$) (Table 45). This is a drop of 13.4% in reproductive potential when females changed mates. Similarly, new partners

TABLE 45. The influence of change or retention of the pair bond on the clutch size

	No. clutches considered	No. eggs laid	Mean clutch size	S.D.
Retained pair bond	121	244	2.02	0.46
Changed pair bond	24	42	1.75	0.43

Note. $t = 2.6537$, d.f. $= 143$, $p = 0.01 - 0.005$

of males changing mates laid significantly smaller clutches than partners of males retaining mates (Table 46). Coulson (1966) has shown an average difference of 0.15 of an egg, in addition he found that there is a progressive increase in the average clutch size with increased breeding experience both in birds which changed mates and in birds that retained the mate from the previous season.

TABLE 46. Clutch size of new partners of males changing mates compared with the clutch size of gulls retaining mates

	No. clutches considered	No. eggs laid	Mean clutch size	S.D.
Retained pair bond	121	244	2.02	0.46
Changed pair bond	27	48	1.78	0.42

Note. $t = 2.4879$, d.f. = 146, $p = 0.025 - 0.010$

6.4.(iv) Size of eggs

Table 47 summarises the length, width and volume of eggs laid by females changing and retaining mates. The volume of eggs was computed from the equation, volume = 0.4825 x length x breadth^2. The value of the constant was determined empirically by the water displacement using 12 eggs.

The constant obtained is similar to values obtained by other workers. Barth (1953) quotes figures between 0.445 and 0.519 from various authors, Coulson (1963) obtained a constant of 0.4866 for the egg of the Kittiwake Gull *Rissa tridactyla* and Stonehouse (1963) derived values from 0.399 to 0.405 for a number of species, the mean value for all species being 0.404.

Among females retaining mates, the length and volume of eggs are significantly larger than for females changing mates.

TABLE 47. Influence of retention and change of mate on egg size

	Pair bond retained				Pair bond changed			
	No. females	No. eggs	Mean	S.D.	No. females	No. eggs	Mean	S.D.
Width of egg	42	82	37.97	1.66	11	20	37.74	0.67
Length of egg	42	82	52.86	1.97	11	20	52.29	1.46
Volume of egg	42	82	36.87	4.01	11	20	35.97	1.98

6.4.(v) Breeding success

No significant difference in breeding success was found between females changing or retaining mates (Table 48). This aspect, however, requires further study since Coulson (1966) has shown significant changes in the proportion of eggs producing fledged young between birds which have changed or retained their mates. Kittiwake Gulls changing mates were on average 13% less successful than those which retained them; the lower breeding success was entirely caused by a failure to hatch the eggs.

TABLE 48. Breeding success of females retaining and changing the pair bond

	Retained mate	Changed mate
Number females	78	16
Number eggs laid	160	27
Number hatched	93 (58.1%)	15 (55.6%)
Number chicks fledged	72 (45.0%)	13 (48.1%)
Number fledged/pair	0.92	0.81

Note. X^2 (% hatched) = 0.1073, d.f. = 1, p = 0.75
X^2 (% fledged) = 0.0923, d.f. = 1, p = 0.90

6.5 Influence of clutch size and brood size

6.5.(i) Breeding success

Table 49 shows that hatching success is greater in two and three egg clutches than in single egg clutches. Similar

TABLE 49. Influence of clutch size on breeding success

Clutch size	No. eggs laid	No. eggs predated	No. eggs hatched	No. chicks fledged
1	174	45 (25.9%)	111 (63.8%)	91 (52.3%)
2	1734	278 (16.0%)	1222 (70.5%)	1014 (58.5%)
3	282	38 (13.5%)	203 (72.0%)	157 (55.7%)
4	16	0	11 (68.8%)	7 (43.8%)

TABLE 50. Survival of young Red-billed Gulls in relation to the date of hatching and brood size

(a) Chicks banded 1965-66

Date of hatching	1 Chick broods		2 Chick broods		3 Chick broods	
	No. banded	No. recovered	No. banded	No. recovered	No. banded	No. recovered
24-30 Oct.			2			
31- 6 Nov.	5	1 (20.0%)	36	4 (11.1%)	3	0
7-13 Nov.	14	1 (7.1%)	120	25 (20.8%)	28	3 (10.7%)
14-20 Nov.	7	4 (57.1%)	58	14 (24.1%)	11	6 (54.5%)
21-27 Nov.	12	1 (8.3%)	80	8 (10.0%)	10	1 (10.0%)
28- 4 Dec.	10	3 (30.0%)	56	4 (7.1%)	9	0
5-11 Dec.	9	0	40	1 (2.5%)	-	-
12-18 Dec.	8	1 (12.5%)	25	2 (8.0%)	9	0
19-25 Dec.	4	0	15	2 (13.3%)		
Total	69	11 (15.9%)	432	60 (13.9%)	70	10 (14.3%)

(b) Chicks banded 1967-68

Date of hatching	1 Chick broods		2 Chick broods		3 Chick broods	
	No. banded	No. recovered	No. banded	No. recovered	No. banded	No. recovered
31- 6 Nov.	5	0	31	6 (19.4%)	1	0
7-13 Nov.	4	3 (75.0%)	82	11 (13.4%)	21	8 (38.1%)
14-20 Nov.	21	4 (19.0%)	176	33 (18.8%)	29	8 (27.6%)
21-27 Nov.	31	3 (9.7%)	177	34 (19.2%)	26	1 (3.8%)
28- 4 Dec.	16	0	58	5 (8.6%)	11	1 (9.1%)
5-11 Dec.	8	1 (12.5%)	43	5 (11.6%)	9	0
12-18 Dec.	14	0	67	8 (11.9%)	12	1 (8.3%)
19-25 Dec.	7	0	18	0		
26- 1 Jan.			9	3 (33.3%)		
Total	106	11 (10.4%)	661	105 (15.9%)	109	19 (17.4%)

(c) Chicks banded 1968-69

Date of hatching	1 Chick broods		2 Chick broods		3 Chick broods	
	No. banded	No. recovered	No. banded	No. recovered	No. banded	No. recovered
17-23 Oct.			2	0		
24-30 Oct.			1	0	2	0
31- 6 Nov.			17	2 (11.8%)	-	-
7-13 Nov.	59	9 (15.3%)	402	41 (10.2%)	67	8 (11.9%)
14-20 Nov.	40	7 (17.5%)	276	23 (8.3%)	51	4 (7.8%)
21-27 Nov.	57	2 (3.5%)	252	12 (4.8%)	39	2 (5.1%)
28- 4 Dec.	40	1 (2.5%)	122	6 (4.9%)	21	0
5-11 Dec.	33	2 (6.1%)	194	9 (4.6%)	6	0
12-18 Dec.	33	0	139	2 (1.4%)	9	0
19-25 Dec.	27	0	31	1 (3.2%)	5	0
26- 1 Jan.	22	0	119	8 (6.7%)	12	1 (8.3%)
2- 8 Jan.	10	0	32	0	3	0
9-15 Jan.	6	0	44	0		
16-22 Jan.	-	-	4	0		
Total	329	21 (6.4%)	1635	104 (6.4%)	215	13 (6.0%)

results have been obtained for Herring Gulls Larus argentatus (Paynter, 1949; Harris, 1964b; and Brown, 1967a).

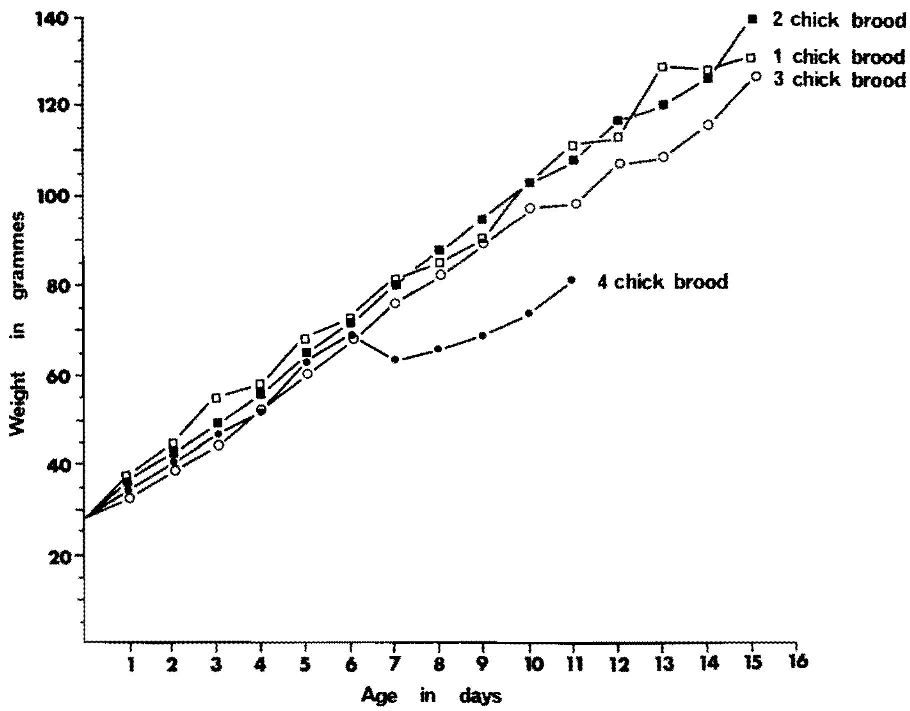
Brown (1967a) considers that small clutches present inadequate stimuli to incubating Herring Gulls and Lesser Black-backed Gulls Larus fuscus since they perform more settling movements when incubating clutches of one than clutches of three. Beer (1961) has also found a lower incubation drive in Black-headed Gulls Larus ridibundus incubating single egg clutches. Brown (1967a) considers that because single egg clutches present inadequate stimuli to the incubating bird, there is the possibility that embryos will die because they become chilled, or are eaten because the parents leave the egg unguarded.

The brood size of three was the largest the adults could normally feed. Artificially raised four chick broods had a slower mean growth rate than smaller broods, and were obviously beyond the capability of parents (Figure 17). This is in accordance with Lack's (1954) argument that natural selection operates in favour of optimum brood sizes, since larger than optimum clutches produce fewer surviving offspring.

Asynchronous hatching is a means of adjusting the brood size to an unpredictable food supply (Lack, 1954). In general younger members of a brood receive food when the older chicks are satisfied (Snow, 1955; Ward, 1965a). The Red-billed Gull chick hatched last often lags behind in growth rate and when the food supply is limited the chick loses weight and dies. If parents obtain plenty of food the youngest chick maintains a similar growth rate to that of older chicks.

6.5.(ii) Post-fledging survival

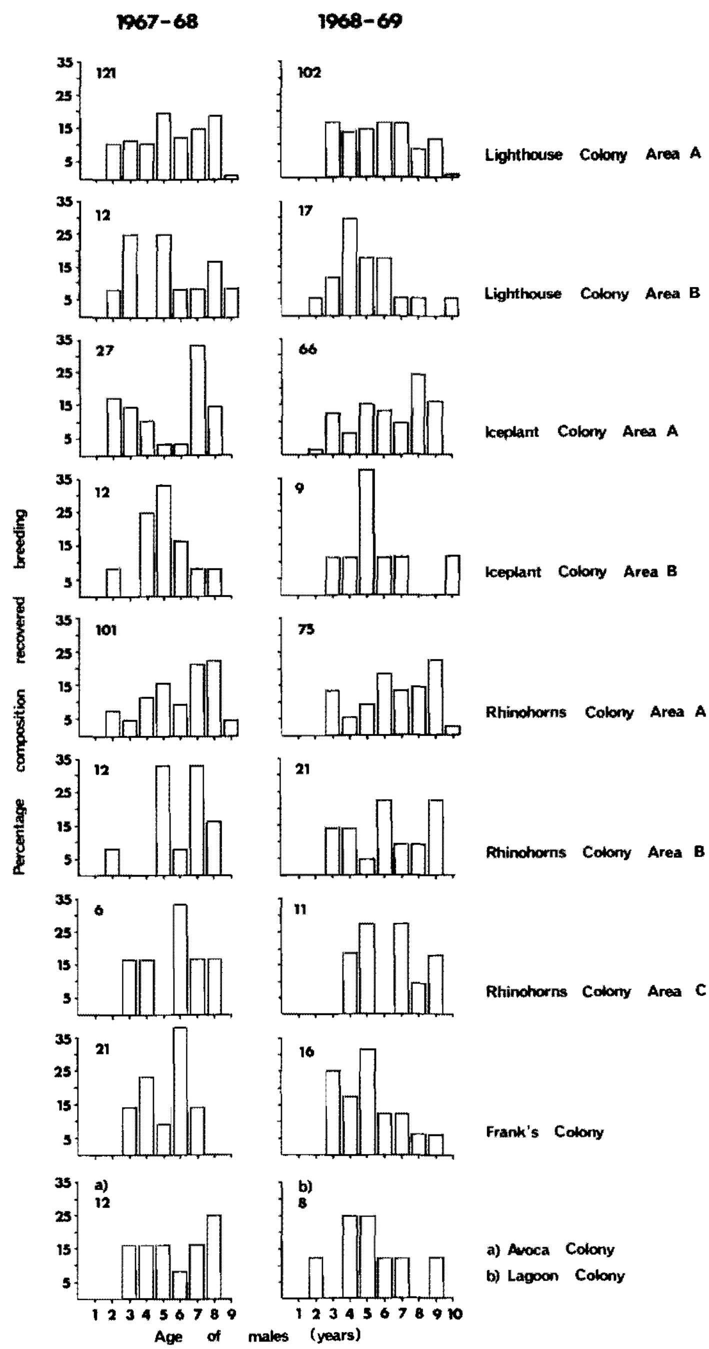
The survival rate of young Red-billed Gulls in relation to brood size is shown in Table 50. Over the complete season



140
120
100
80
60
40
20
Weight in grammes
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Age in days
2 chick brood
1 chick brood
3 chick brood
4 chick brood

FIGURE 17. Mean growth rate of different sized broods. Four chick broods were artificially raised three egg clutches. The means are based on at least five broods.

the post-fledging survival was similar from broods of all sizes. Löhrl (1957) and Curio (1958) also found this for the Collared Flycatcher, Ficedula albicollis. These findings do not support Lack's (1954) view "that the clutch size of each species of bird has been adapted by natural selection to correspond with the largest number of young for which the parents can, on the average, provide enough food." Lack's theory, however, is based on the probability that "on average" the optimum clutch is the most productive. The striking feature of Table 50 is that in different years different brood sizes hatching at the same time are more productive than others. This may result because conditions for rearing young vary so much from one year to the other. Perrins (1965) believes that this may be the reason why a wide range of clutch sizes persists in the population, presumably because each has been the most productive too frequently for it to have been eliminated by natural selection. Alternatively, Lack (1966) has added the provision "that if larger clutches tend to be laid chiefly when there is a greater chance of larger broods being raised, the average clutch will probably not be that from which, on the average, most young are raised per brood." This is a possibility in the Red-billed Gull, since three chick broods in some years are more productive than smaller clutches, and this corresponds to the time when the greatest number of three egg clutches are laid.



1967-68
1968-69
121
102
Lighthouse Colony Area A
12
17
Lighthouse Colony Area B
27
66
Iceplant Colony Area A
12
9
Iceplant Colony Area B
101
75
Rhinohorns Colony Area A
12
21
Rhinohorns Colony Area B
6
11
Rhinohorns Colony Area C
21
16
Frank's Colony
a) 12
b) 8
a) Avoca Colony
b) Lagoon Colony
Percentage composition recovered breeding
Age of males (years)

FIGURE 18. Age structures of colonies and study areas. Newly established colonies are: Frank's, Lagoon and Avoca.

TABLE 51. Proportion of gulls breeding at newly established colonies that are known to have bred at other colonies in previous seasons

	Males				Females			
	1967-68		1968-69		1967-68		1968-69	
	No. males recovered	No. bred at other areas	No. males recovered	No. bred at other areas	No. females recovered	No. bred at other areas	No. females recovered	No. bred at other areas
Frank's	21	9 (42.9%)	16	4 (25.0%)	18	4 (22.2%)	14	4 (28.6%)
Avoca	12	1 (8.3%)	2	0	5	0	1	0
Lagoon	3	0	12	6 (50.0%)	2	1 (50.0%)	6	4 (66.7%)
Total	36	10 (27.8%)	30	10 (33.3%)	25	5 (20.0%)	21	8 (38.1%)

6.6 Influence of new and established colonies

6.6.(i) Age structure

Between 1964 and 1968 three new colonies have been established; the Avoca Colony in 1964-65 and Frank's and Lagoon Colonies in 1967-68.

For the Kittiwake Gull *Rissa tridactyla* (Coulson & White, 1956, 1960) it has been assumed that gulls establishing new colonies are predominately young birds. This is not true for the Red-billed Gull (Figure 18). The age structures have been based on the age of the male, because it is believed that males are mainly responsible for the selection of nest sites. At Kaikoura the new colonies were not composed principally of young males but of males aged from two to nine years. Furthermore, these new colonies are not made up of inexperienced breeders. Several of the gulls breeding at the new colonies have been recovered breeding in different colonies in previous years (Table 51).

The age structures differed markedly between areas within seasons, and in many cases the structures differed for the same area between seasons. The small samples of some areas probably contribute to the marked differences between seasons. In the Lighthouse Colony Area A, and Rhinohorns Colony Area A where samples are large, the structures were similar. This is what would be expected since gulls show a marked attachment to areas where they have bred previously (Table 52).

TABLE 53. Breeding success at new and established nesting sites

Colony	Year first used	1967-68 Season No. nests	No. eggs laid	Per cent fledged	No. fledged per pair	1968-69 Season No. nests	No. eggs laid	Per cent fledged	No. fledged per pair
Avoca	1965-66	107	195	28.7%	0.52	20	29	0.0%	0.00
Lagoon	1967-68	61	94	0.0%	0.00	95	164	24.4%	0.43
Frank's	1967-68	112	203	42.9%	0.78	96	187	39.0%	0.76
Total		280	492	29.1%	0.51	211	380	29.7%	0.54
"Old colonies"		584	1131	61.4%	1.19	635	1246	56.5%	1.11

TABLE 54. Causes of egg failure in new and established colonies

Colony	Year first used	No. nests	No. eggs laid	Per cent destroyed by swamping	Per cent eggs predated	Per cent hatched
1967-68						
Avoca	1965-66	107	195	29.7%	9.7%	55.4%
Lagoon	1967-68	61	94	81.9%	9.6%	7.4%
Frank's	1967-68	112	203	18.7%	25.1%	46.8%
"Old colonies"		584	1131	4.8%	13.2%	61.4%
1968-69						
Avoca	1965-66	20	29	0.0%	100.0%	0.0%
Lagoon	1967-68	95	164	51.8%	14.0%	31.1%
Frank's	1967-68	96	187	40.1%	13.9%	43.9%
"Old colonies"		635	1246	6.5%	16.9%	68.6%

TABLE 52. Proportion of gulls breeding at the same nest area in successive seasons

Sex	No. gulls considered	Same colony same area	Same colony different area	Different colony
Male	148	106 (71.6%)	19 (12.8%)	23 (15.6%)
Female	145	102 (70.3%)	19 (13.1%)	24 (16.6%)

6.6.(ii) Breeding success

The breeding success in newly established and old colonies is compared in Table 53. Gulls nesting in newly established colonies were strikingly less successful than gulls nesting in old colonies. The mean number of young fledged per pair at new colonies in the 1967-68 and 1968-69 seasons was 0.52 compared with 1.15 for old colonies. A similar marked difference in breeding success between established nest sites and new sites was recorded by Snow (1960) for the Shag *Phalacrocorax aristotelis*.

The main mortality agents in the new Red-billed Gull colonies, were predation and swamping (Table 54). In two of the colonies, in different years, no young were raised. In the Avoca Colony in 1968-69 the failure was due to vandals firing a shot-gun into the colony, killing twelve adult gulls and causing the remainder to desert.

As can be seen from Table 55, the greatest loss involved the failure of the complete clutch or an incomplete clutch.

The lower breeding success at newly established colonies is not a reflection of the breeding age of the gulls but to the poor habitats, which are susceptible to flooding.

TABLE 55. Causes of partial or whole failure of clutches at new and old colonies

Year	Colony	Total No. clutches	Whole clutch failed	No. of whole clutches failing to hatch due to: Predation	Swamping
1967-68	Avoca	107	36	7 (19.4%)	26 (72.2%)
	Lagoon	61	28	3 (10.7%)	25 (89.3%)
	Frank's	112	35	24 (68.6%)	11 (31.4%)
	"All old colonies"	584	92	54 (58.7%)	27 (29.3%)
1968-69	Avoca	20	10	10 (100%)	-
	Lagoon	95	44	8 (18.2%)	33 (75.0%)
	Frank's	96	46	11 (23.9%)	34 (73.9%)
	"All old colonies"	635	131	59 (45.0%)	22 (16.8%)

Year	Colony	Total No. clutches	Partial clutch failed	No. of partial clutches failing to hatch due to: Predation	Swamping
1967-68	Avoca	107	7	1 (14.3%)	-
	Lagoon	61	1	-	-
	Frank's	112	13	3 (23.1%)	-
	"All old colonies"	584	70	14 (20.0%)	-
1968-69	Avoca	20	-	-	-
	Lagoon	95	2	-	2 (100%)
	Frank's	96	5	1 (20.0%)	-
	"All old colonies"	635	64	18 (28.1%)	-

Year	Colony	Total No. clutches	Incomplete clutches destroyed	No. of incomplete clutches failing to hatch due to: Predation	Swamping
1967-68	Avoca	107	9	3 (33.3%)	6 (66.6%)
	Lagoon	61	27	2 (7.4%)	25 (92.6%)
	Frank's	112	25	16 (64.0%)	8 (32.0%)
	"All old colonies"	584	11	11 (100%)	-
1968-69	Avoca	20	9	9 (100%)	-
	Lagoon	95	21	7 (33.3%)	14 (66.6%)
	Frank's	96	7	3 (42.9%)	4 (57.1%)
	"All old colonies"	635	18	14 (73.7%)	3 (16.7%)

6.7 Replacement clutches

Replacement clutches are common in seabirds and the Red-billed Gull is no exception. Re-laying generally followed egg losses by predation and swamping. Only occasionally were replacement clutches laid after chicks had died (Mills, 1967). In most instances re-nesting took place at the same nest site. The earliest re-laying was seven days after the disappearance of the first clutch and the longest was 33 days.

6.7.(i) Clutch size

Although the mean clutch size of replacement clutches is statistically smaller than the original clutch, only 28% of the females laid smaller clutches than the original (Table 56).

TABLE 56. Clutch size of replacement clutches

Completed first clutch	Completed replacement clutches 1	2	3	Total	% less	% same	% more
1	2	5		7		28.6%	71.4%
2	21	48	3	72	29.2%	66.6%	4.2%
3		3	2	5	60.0%	40.0%	
Total	23	56	5	84	28.6%	61.9%	9.5%

Note. Average clutch size of first clutches 1.98 ± 0.38

Average clutch size of replacement clutches 1.79 ± 0.54

t (First - replacement clutches) = 2.6408, d.f. = 166, p = 0.01-0.001

The replacement clutches show the same seasonal decrease in size as original clutches (Table 57).

TABLE 57. Seasonal variation of replacement clutches

Date	Replacement clutch size 1	2	3	Total	Mean clutch
3- 9 Oct.					
10-16					
17-23					
24-30	1	1		2	1.50
31- 6 Nov.		2		2	2.00
7-13		4	2	6	2.33
14-20	1	9	2	12	2.08
21-27	3	4	1	8	1.75
28- 4 Dec.	2	12		14	1.86
5-11	4	12		16	1.75
12-18	7	10		17	1.59
19-25	6	4		10	1.40
26- 1 Jan.	1			1	1.00
2- 8					
9-15 Jan.		2		2	2.00
Total				90	1.78

Only older gulls lay replacement clutches, perhaps because younger gulls (which normally breed late in the season) are unable to obtain sufficient food to manufacture eggs.

6.7.(ii) Breeding success

The breeding success of replacement clutches was markedly higher than that for first clutches in the 1967-68 season but only slightly so in 1968-69 (Table 58).

TABLE 58. Breeding success of replacement clutches

	No. gulls considered	No. eggs laid	No. hatched	Per cent hatched	No. fledged	Per cent fledged	No. fledged per pair
1967-68	12	22	21	95.5%	20	90.9%	1.67
1968-69	46	87	54	62.1%	46	52.9%	1.00
Total	58	109	75	68.8%	66	60.6%	1.14

6.8 Deferred maturity

Sea birds normally do not breed until they are two years old or more. The reasons for this long prematurity period have been subject to speculation. The phenomenon is referred to as deferred maturity. Wynne-Edwards (1962) considers that delayed development has been evolved in long-lived marine species to reduce productivity and prevent over population.

The Red-billed Gull is capable of breeding at two years but the majority do not do so until the third or fourth year. The duration of the prematurity period in the Red-billed Gull is similar to that of other long-lived seabirds. For example, the Shag Phalacrocorax aristotelis (Snow, 1960) breeds first at three - four years, and the Cormorant Phalacrocorax carbo (Kortlandt, 1942) at three or sometimes even four or five years. In the Kittiwake Gull Rissa tridactyla, Coulson (1966) found that breeding took place mainly between three and five years, while the age of first breeding in the Short-tailed Shearwater, Puffinus tenuirostris, occurred between five and eight years, with a mean of 5.9 years (Serventy, 1967).

In the Red-billed Gull, females delay breeding longer than males. In other species of birds it is usually females which mature earliest (see Section 5.4). The evidence in this study indicates that females survive better than males; the reverse has been found in other studies. Thus, in this study and in others the sex which survives best has the longest prematurity period, perhaps because they outnumber the opposite sex and so have difficulty in obtaining partners. Table 59 shows the sex and age composition of the prebreeding

TABLE 59. Comparison of males and females of different ages in the prebreeding and breeding populations of the 1965-66 season

	No. recovered	Percent composition in population					
		2	3	4	5	6	7 years
Males							
Prebreeding	48	14.6	22.9	18.8	16.7	18.8	8.3
Breeding	322	5.6	18.0	13.7	23.9	23.6	15.2
Females							
Prebreeding	47	14.9	29.8	27.7	12.8	10.6	4.3
Breeding	220	1.8	23.2	20.0	23.2	19.5	12.3

and breeding populations. Theoretically, there is an equal chance of males and females of any age group breeding, however, younger gulls (although present at Kaikoura) are not participating in breeding as much as are older ones. In both the male and female breeding populations there are smaller proportions found in the two, three and four year age classes than are present in the general population. Banded gulls over four years make up only 43.8% of the male and only 27.7% of the female pre-breeding population, but contribute 62.7% of the male and 55.0% of the female breeding population. It appears that older females are better able to obtain partners than younger females. This, however, would not explain the failure of young males to breed since there is not a surplus of males in the population. This could be due to difficulties in obtaining nest sites or their inability to obtain sufficient food to attain breeding condition.

Wynne-Edwards (1962) emphasises the importance of nest site tenure; he considers that colonies have recognised boundaries, not necessarily physical, which inhibit by tradition breeding in a new place, even when there is a surplus of adult birds. In the Red-billed Gull, there is competition for the best nest sites - on higher ground and central areas - but no evidence for "traditional boundaries". On the contrary, new areas within colonies and new colonies are periodically being established.

Since nesting sites cannot be considered a significant factor in restricting breeding the alternative of competition for food seems probable. Ashmole (1963), Carrick & Murray (1964), Murton, Isaacson & Westwood (1966) have considered this. They believe that intraspecific competition during feeding denies food to less experienced birds. Ashmole, with particular reference to tropical oceanic seabirds, suggested that the competition is for the restricted amounts of food that become available rather than for the total resources.

There is evidence which indicates that when food is abundant and aggression low, birds of immature plumage have bred. This has been found in the Pomarine Jaeger Stercorarius pomarinus (Pileika et al, 1955) and the Magpie Gymnorhina tibicen (Carrick & Murray, 1964). Such a situation may be defined as enhanced maturity.

Lack (1968) considers that the only tenable view, if one accepts natural selection, is that "birds have evolved physiological regulating factors to prevent earlier maturity because this, on balance, enables them to leave more offspring than if they mature earlier." He adds "this view implies, first, that any individuals which attempt to breed when younger are unlikely to suceed, and secondly that the attempt to breed exposes the birds to a higher mortality than if they do not attempt to breed." Further research would be required to prove or disprove Lack's hypothesis. However, as shown in Section 5.1, there is considerable evidence to suggest that the long prematurity of Red-billed Gulls may result from younger birds being unable to obtain sufficient food to attain breeding condition.

6.9 Immigration and emigration

As shown in Section 5.3 there is very little immigration into the Kaikoura breeding population of gulls that were hatched at other localities. Losses from the population by emigration of chicks hatched at Kaikoura, is greater than the gain from immigration. At Lake Grassmere (82 miles north of Kaikoura), a colony of 250 - 350 pairs, 51 gulls which were banded at Kaikoura as nestlings, have been recovered breeding there between the 1961-62 and 1964-65 seasons by Mr S.R. Kennington. Regular recovering of banded gulls has not been undertaken at other colonies, but small numbers of Kaikoura gulls have been recovered breeding in colonies at Nawhi Point, Nelson, Kapiti Island and the Waitaki River mouth. Not all of these gulls are lost permanently from the population since some have been recovered back at Kaikoura in subsequent years.

In view of the surplus of female gulls in the Kaikoura population, it would be of interest to know whether the emigrating gulls are mainly females.

TABLE 60. Causes of death in age classes

Category	Age in completed years									Total
	Juv.	1	2	3	4	5	6	7	8	
Cause unknown	158	34	24	20	23	9	4	7	2	281
Shot- control measures	3		1			1				5
Found shot	4	5	3	1	1	1		1		16
On road (car)	36	5	3	3	1	3	1	1		53
On railway (train)	3									3
On airport					1					1
Injured and killed	15	4	4			2				25
Caught in fishing line or net	2	2	1	2		1				8
Oiled		1								1
Drowned	3	1								4
Bird of prey	1									1
Stoat	66	1	1	1	1	1	1			73
Dog			1							1
Died on breeding colony as adult				1	2	1	2		1	8
Died on breeding colony as juvenile	4									4
Collision with overhead wires		1								1
Exhausted or ill	3									3
Hit by golf ball				1						1
Choked on fish								1		1
Killed (experimental reasons)		8	29	6	12	7				68
Killed during capture- alpha chloralose			1		2		1			4
Band found only	1									1
Total										563

7. MORTALITY

7.1 Causes of mortality

The data in this section are based mainly on recoveries of banded birds reported by the public.

Smith (1959) emphasises that although some idea of the causes of death of banded birds can be gained from details of recovery reports, equal significance cannot be given to all the recoveries. Paynter (1947) argues that deaths associated with human activities will be adequately recorded, but birds killed by predation, disease and other causes will be recovered only by chance.

Of the 563 reported recoveries nearly half (281) died from unknown causes. The main causes of death in relation to age are shown in Table 60.

Although the Red-billed Gull is protected under the Wildlife Act (1953) a small proportion inevitably is shot (2.8%). If gulls "shot for control measures" are included, the proportion of juveniles amounts to 33%. Similarly, in the Lesser Black-backed Gull *Larus fuscus gracellsii* (Lack, 1943) and the Shag *Phalacrocorax aristotelis* (Potts, 1969) juveniles feature prominently in shot recoveries.

As with recoveries of shot gulls, greater numbers of juveniles have been reported involved in collisions with cars and trains. Van Tets (1968) believes that this may be because of inexperience and lack of caution. The number of gulls killed by automobiles probably represents the proportion dying from this cause of the total number banded, as the chances of a gull being recovered from such a death is comparatively high.

Of the 75 reported deaths due to predation, 73 were caused by Stoats *Mustela erminea*. Adults are vulnerable only during the breeding period, because at other times they

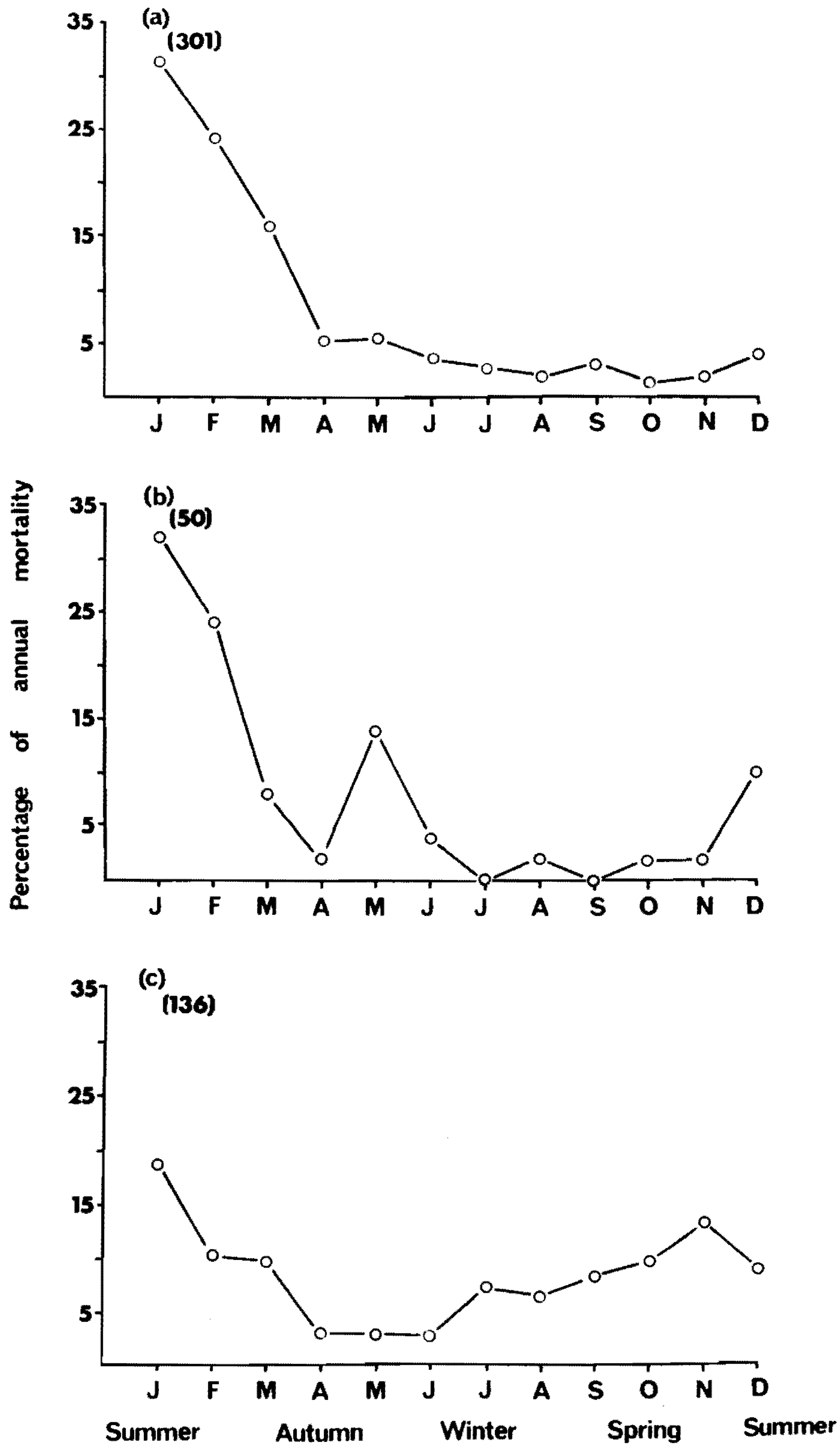

(a)
(301)
(b)
(50)
(c)
(136)
Percentage of annual mortality
35
25
15
5
J F M A M J J A S O N D
Summer
Autumn
Winter
Spring
Summer

FIGURE 19. Seasonal distribution of mortality: (a) gulls less than year old, (b) gulls one year of age, (c) gulls two years of age and older.

roost mainly on offshore stacks inaccessible to ground predators.

7.2 Seasonal distribution of mortality

The recoveries excluded from the analysis include "gulls killed for scientific purposes", "band found only" and "band attached to skeleton".

The highest adult mortality (gulls more than two years after fledging) occurred from early spring to late summer and the lowest in winter (Figure 19 c). The pattern of mortality of gulls less than a year after fledging differs from that of adults (Figure 19 a). Mortality is highest immediately upon fledging and decreases as the year progresses. Mortality of year old gulls is highest in January with a secondary peak in May (Figure 19 b).

These patterns differ from those derived for the Red-billed Gull by van Tets (1968), but are similar to those determined for the closely related Silver Gull *Larus novaehollandiae* in South-eastern Australia by the same author. However, the mortality patterns van Tets derived for the Red-billed Gull are not comparable with those determined for that species in the present study as they are based on recoveries published in Banding Reports and are subject to errors, since these often give the outstanding recoveries only, usually in terms of the age of the bird or the distance from the banding locality; thus the recoveries are not randomly distributed in time or space (Robertson, pers. comm.).

Bias is likely in the seasonal reporting rate. The chances of finding a dead bird depend mainly upon where it dies (Potts, 1969). A gull dying on a remote coast is less likely to be found than one which dies at a coastal resort. The seasonal distribution of recoveries is more likely to indicate human activity than gull mortality (Kadlec & Drury, 1968). Van Tets (1968), studying the seasonal mortality of several gull species, believes that there are sufficient divergencies in the seasonal recovery rates of young and old gulls to discount the possibility that variations are mainly due to the seasonal fluctuations in habits and distributions of finders. However, it must be mentioned that bias is likely in both the present study and that made by van Tets. When adults withdraw to the breeding colonies in July and early August the younger gulls remain behind in the "over-wintering" areas. Consequently, the chances of recovering adults, which are congregated at the breeding grounds, are greater than those of recovering juveniles which are dispersed over a wide area.

TABLE 61. Recoveries of Kaikoura banded gulls remaining at Christchurch in October, November, and December 1968

Year of banding	No. banded	No. recovered	Corrected to 2000/year	Percentage composition
1958-59	871	-	-	-
1959-60	2223	4	4	6.8%
1960-61	2011	3	3	5.1%
1961-62	2036	1	1	1.7%
1962-63	1989	2	2	3.3%
1963-64	2065	1	1	1.7%
1964-65	2684	5	4	6.8%
1965-66	3403	5	3	5.1%
1966-67	1529	1	1	1.7%
1967-68	1240	25	40	67.8%
		47	59	100.0%

If the differences are real, the seasonal recovery rates of young and adult gulls probably result from differences in their ecology. In the non-breeding season the gulls are distributed over a wide area, up to 350 miles from the natal colony. In late June and July when the adults return to the colonies the juveniles remain in the "over-wintering" area (Table 61). With the departure of the adults, competition for food is reduced among the younger gulls. Adults returning to Kaikoura face increased competition for food near the colonies and consequently unsuccessful gulls perish. The demands on the gulls and the food supply increase when the young hatch. It is apparent from the loss in weight of parents in the post-breeding period (Table 62), that the raising of young has made severe demands

TABLE 62. Changes in body weight in the breeding and the post-breeding period

	Males			Females		
Month	No. males	Mean weight	S.D.	No. females	Mean weight	S.D.
December	36	307.8	17.7	27	273.1	14.6
January	40	288.4	20.0	24	254.6	16.7
February	36	262.9	15.2	26	234.0	11.0
March	19	299.5	26.5	14	270.7	17.6

upon them. The highest mortality corresponds to the period of loss of condition. The decrease in the relative abundance of plankton at this time, coupled with the fledging of the chicks, places excessive demands on the food supply.

In January, adults and fledgings begin to disperse from the Kaikoura colonies. By distributing themselves widely the gulls are able to reduce the competition for food and regain lost condition. Carrick & Murray (1964) consider that recently fledged gulls are at a disadvantage compared with older gulls, and this is confirmed by the high post-fledging mortality in this study. The high mortality of year old gulls in January and February coincides with the arrival of adults and juveniles. Gull mortality increases at the age at which gulls can first attempt to breed.

8. SEX SPECIFIC SURVIVAL

There are several problems associated with estimating survival from recoveries of live Red-billed Gulls. With the exception of the samples obtained in the pre-breeding period by spotlighting, females are under-represented in all samples, consequently composite life tables can not be used to compare sex specific survival. The loss of bands from gulls prevents the application of Jolly's (1965) stochastic model to estimate survival, and furthermore the method can not even be applied to cohorts where band loss was minimal, because in later years colour banding was introduced which alters the recapture rate. It is much easier to find and identify colour marked gulls than others.

The best time to collect data for analysis of sex specific mortality is in the prebreeding period, but unfortunately, too few recoveries were made then to allow mortality to be assessed. The only alternative is to assess mortality from recoveries made in the breeding season.

The survival data according to age class are given in Table 63. Surprisingly, the survival rate of males in most age classes exceeds that of females. This is contrary to expectation as earlier findings show a surplus of females in the population. It has been shown in Section 4.1, that unbanded females are more numerous than unbanded males. This could be due to immigration of unbanded females or emigration of unbanded males both are unlikely. Samples of banded gulls captured in the prebreeding period did not depart from a 50:50 sex ratio, although in fact banded females were known to be under-represented in the older age classes since band loss is greater from females. Consequently, two different sampling programmes have indicated a surplus of females in the population,

Considering the evidence, it seems probable that females

TABLE 63. Differential survival of sex from the 1967-68 breeding season to the 1968-69 season

Year banding cohort	Males		Females	
	No. recovered in 1967-68	No. recovered in 1968-69	No. recovered in 1967-68	No. recovered in 1968-69
1958-59	7	7 (100.0%)	6	4 (66.7%)
1959-60	56	36 (64.3%)	32	22 (68.8%)
1960-61	59	39 (66.1%)	49	30 (61.2%)
1961-62	44	30 (68.2%)	30	24 (80.0%)
1962-63	51	34 (66.7%)	41	24 (58.6%)
1963-64	40	26 (65.0%)	24	13 (54.2%)
1964-65	32	20 (62.5%)	19	4 (21.1%)
1965-66	31	18 (58.0%)	3	0 (0.0%)

are surviving better than males, and that a bias exists in the recapturing of females from the previous season. A possible explanation is that when the pair bond is changed the male is more likely to breed again and so is more likely to be recovered than the female (Table 64). However, the differences are not statistically significant and so further information is required to confirm this.

The question arises whether sufficient regard has been given in other studies to sampling biases. Probably the most important aspect other researchers have not considered is the possibility of greater loss of bands from females.

An attempt has been made to construct a life table in Table 63 by excluding the female recoveries. The analysis concerns the survival of cohorts which have minimal band loss (Type D). Allowance has been made for gulls being

TABLE 64. Proportion of males and females not recovered after the mate of the previous season changed the pair bond

	No. changed mates	No. mates not recovered breeding	No. mates recovered breeding
Females	24	17 (70.8%)	7 (29.2%)
Males	28	21 (75.0%)	7 (25.0%)

Fisher's exact test, p = 0.9777

TABLE 65. Known male survivors from recovery data

Date banded	No. males banded	Years after banding 1	2	3	4	5	6	7	8	9
1959-60	500					72	64	*	42	35
1960-61	1005				173	164	*	111	96	
1961-62	1000			143	136	*	99	88		
Total recoveries				143	309	236	163	199	138	35
Number at risk				1000	2005	1505	1500	2005	1505	500
Proportion surviving				.1430	.1541	.1568	.1087	.0993	.0917	.0700
If annual survival rate is P, these proportions equal		p1	p2	p3	p4	p5	p6	p7	p8	p9
Thus P equals				.523	.627	.690	.691	.719	.742	.744
					Mean P = 0.6776					

Note. * No recoveries made.

alive previous to the date of last capture or sighting. An assumption is made that equal numbers of males and females were banded as chicks. The data show increasing survival with age. The mean annual survival estimate is 0.6776 which is equivalent to an expectation of life of 2.6 years. In Table 66 the survival has been estimated from subsequent

TABLE 66. Calculation of minimum survival of adult male Red-billed Gulls from subsequent recoveries of gulls known to be alive at the breeding grounds in 1967-68

Date banded	No. males recovered in 1967-68	Age in years	Year interval at risk 2-3	3-4	4-5	5-6	6-7	7-8	8-9
1959-60	55	8							39
1960-61	59	7						46	
1961-62	44	6					35		
1962-63	51	5				42			
1963-64	40	4			32				
1964-65	32	3		23					
1965-66	31	2	21						
Total recoveries			21	23	32	42	35	46	39
No. at risk			31	32	40	51	44	59	55
Proportion surviving			.677	.719	.800	.824	.795	.780	.709

recaptures or sightings of gulls from cohorts of known age which were alive at the breeding grounds in the 1967-68 breeding season. All gulls were rebanded with a numbered aluminium band and a single colour band. A second order polynomial curve fitted to the survival estimates gives the form:

$$y = 35.62 + 15.83x - 1.37x^2.$$

The polynomial gives a good fit for the range but extrapolation of the survival rate for older birds is unsatisfactory since it gives a maximum life span of only 12.1 years, which is obviously an underestimate. More data points are required, especially for older gulls, for a realistic survival curve. If we assume that survival is constant irrespective of age, the probability the bird survives one year is given by:

$$\text{Estimate} = \frac{\text{total birds survive for one year}}{\text{total birds at risk for one year}}$$

$$= 0.7301 = \text{mean annual survival rate.}$$

$$\text{Life expectancy} = \frac{1 + \text{mean annual survival}}{2(1 - \text{mean annual survival})}$$

$$= 3.20 \text{ years}$$

Since the banding data shows that 14.3% of the male chicks survive to breeding age (2 years), and 73% of the adult males survive, 188.8 male chicks per 100 adult male gulls would be required to be hatched in order to maintain a stable population. This is an unacceptable estimate considering the population increase. Obviously the survival estimates are too low because a number of banded gulls are not being recaptured.

9. DISCUSSION AND CONCLUSIONS

In the previous sections, factors which influence the breeding biology have been discussed separately. Many of the factors are known to interact so it is appropriate at this stage to examine them collectively. Specific aspects discussed include the laying date, clutch size, and the production and survival of chicks.

Laying date

The date when egg laying commences has a profound effect on several aspects of breeding. It has been shown that the largest clutches are laid early in the season and gulls which commence laying early produce more surviving young. Thus, there is an obvious advantage in breeding as early as possible. Several factors modify the time of laying. No statistical difference was found in laying dates between two and four year old females, but mean differences of 9 days in 1967-68 and 17 days in 1968-69 between three and five year old females were statistically significant. The variability of laying dates within age classes was large, because other factors as well as age are having an effect on the time of laying. One of the most important factors is the retention or change of the pair bond of the previous season. Females retaining the mate of the previous season breed on average 10.2 days earlier than gulls changing mates. For the Kittiwake Gull *Rissa tridactyla*, Coulson (1966) has shown that when older females retain the same mate, the average laying date in progressively older birds advances. In the present study samples of particular age groups retaining mates were too small to ascertain trends of this nature.

While the advantages of retaining the pair bond is obvious, in some cases the breaking of the bond is advantageous. In 50% of pair bond changes the female commenced laying earlier than in the previous season. Coulson (1966) considers "that there may be a degree of incompatibility between individuals which results in unsuccessful breeding and it is clearly an advantage for such pairs to split up in the hope that they will find a new partner who is more suitable." In the Kittiwake Gull Rissa tridactyla, Coulson (1966) found that delayed breeding of gulls changing mates can only in part be due to females tending to take a younger male as a new mate, therefore other factors must be concerned. In this study, it has been shown that some gulls retaining mates are able to leave the colony. Females changing mates must presumably spend time seeking new mates, a difficult task given the female surplus in the population. Females changing mates presumably have less time to feed than females retaining mates. Coulson believes that this can not be the only factor involved since the change of mate in the Kittiwake Gull affected the laying date for at least two seasons afterwards. This matter has not been examined in the Red-billed Gull. To account for the prolonged effect of mate changes, Coulson suggested that the change produces a depressive effect on the breeding biology through a lasting influence on the females' nervous and endocrine systems.

The other factor studied which has a marked effect on the laying date was the age of the male. In general, females of the same age breed earlier in the season with increasing age of the male partner. Female Kittiwake Gulls breeding for the first time, bred 5 days earlier with an experienced male, than if they bred with a male which was breeding for the first time. In the Red-billed Gull the difference is more marked. Two - four year old females laid an average of 18.2 days earlier if they bred with males five years and older than if they bred with two year old males. The difference is highly significant ($p = < 0.001$). This trend is probably due in part to the effects of retention of the breeding partner of the previous season, particularly in females five years and older. However, many of the two - four year old females had not bred previously, and there is a direct effect of the age of the male. The delayed breeding of females with young males may be linked with "courtship feeding". "Courtship feeding" provides an additional food supply for the female at a time when she requires it most. The importance of "courtship feeding" can be assessed from the knowledge that three weeks before egg laying the female spends 81% of the time in the nest territory. Inexperienced males may not be able to forage for food as well as older birds, and any reduction in the quantity or quality of food given to the female may have important consequences.

Perrins (1965, 1970) considers the ultimate factor which prevents late breeders breeding early is lack of food. He believes that the female is probably breeding as soon as she can attain breeding condition, thus birds which breed late do so because they are unable to obtain sufficient food to manufacture eggs at the beginning of the season. This theory would explain the spread of egg laying over an extended period during which gulls gradually attain breeding condition as food becomes more plentiful. It also explains why most late breeders are young birds. This view is strengthened by the weight distribution of gulls breeding in the first seven days after the first egg was laid at the colonies. In these early breeders there is an absence of light gulls which are present in the general population. It is reasonable to assume that these underweight gulls have not reached breeding condition.

Clutch size

The clutch size of the Red-billed Gull is affected by several factors: age of female, age of male, time of laying, and retention or change of the pair bond. As Perrins (1966) has shown for the Great Tit *Parus major*, these may not all influence the bird simultaneously, but several can operate together, either directly or indirectly through the date of laying.

The largest clutches are laid early in the season and there is a progressive decrease in mean clutch size with time. The largest clutches are normally laid by older females. Young females laying at the same time as older females have significantly smaller mean clutches. This is complicated further by the age of the male partner. Females of the same age group tend to lay proportionately larger clutches the older the male partner. As already discussed, "courtship feeding" may play a significant role, since young inexperienced males may provide less food per feed to the female than older males. The other factor investigated in this study which influenced clutch size was retention or change of the pair bond. Females retaining mates laid statistically larger clutches than females changing mates.

Early breeders attain breeding condition and lay the largest clutches prior to the peak abundance of food, while gulls breeding later often attain breeding condition at the peak abundance of food but lay small clutches. This situation is known to occur in many species of birds and has led Lack (1954) and Perrins (1965) to postulate that normally food at the time of laying has no influence on the clutch size. Perrins (1970) cites further evidence which shows that eggs in late clutches of the Great Tit which are larger and heavier than those laid in early clutches. Lack (1954) believes that the clutch size is adapted to the availability of food for the young, but Perrins (1965) disagrees with this interpretation since there is no evidence that birds are able to predict the level of prey populations. Perrins believes instead that the Great Tit Parus major adjusts the clutch size to factors such as the appearance of the habitat.

In the Red-billed Gull it appears more likely that any seasonal modification to the clutch size is a response to the conditions the female is experiencing immediately prior to laying. Lack and Perrins' arguments are not necessarily valid. Because food is more abundant when late breeders lay does not mean that these gulls are able to obtain large quantities of it. In the Woodpigeon, Columba palumbus, Murton, Isaacson & Westwood (1966) have suggested "that if flock size is too high relative to food availability some birds have feeding rates below an optimum threshold and under these conditions they leave the flock to forage elsewhere." It would only be when the food became abundant that the less successful feeders could attain breeding condition. Furthermore, Perrins' (1970) analysis of egg weights is somewhat misleading because it is based on mean weights of clutches, and as it is known that early breeders lay more eggs per clutch than late breeders the total weight of eggs laid by late breeders may be considerably lighter than early clutches. It is the total weight of the clutch that is important. Furthermore, Coulson (1963) has shown that the Kittiwake Gull Rissa tridactyla lays smaller eggs later in the season.

It could be argued that the smaller replacement clutches laid by early breeders later in the season supports the view that the reduction is adapted to the food for the young. This is not necessarily so. It must be emphasised that in the Red-billed Gull only 28% of replacement clutches are smaller than the original. This small proportion may result from physiological limitations related to the difficulty in developing egg follicles after they have regressed (see Harris (1964)). In other words, the small replacement clutches of the early laying birds (presumably the successful competitors) need not reflect difficulties in obtaining food later in the season; these birds may be able to obtain enough food but physiological factors prevent development of the ovules.

Studies of the growth rates of different sized broods show that the maximum brood that adults can successfully nourish is three. In artificially raised four chick broods the growth rate fell well below the rate of smaller brood sizes. In this respect the results support the view put forward by Lack (1966) "that the clutch size is adapted to the largest number of young which the parents can normally raise, the addition of young to make larger broods than normal should result in fewer, not more, young surviving per brood." The post-fledging survival of different size broods, however, is contrary to Lack's views, because survival was similar from broods of all sizes. The same has been demonstrated from band recoveries for the Collared Flycatcher Ficedula albicollis (Löhrl, 1957; Curio, 1958) and the Pied Flycatcher Ficedula hypoleuca (Curio, 1960; v Haartman, 1967). Lack (1966) has added the provision "that if larger clutches tend to be laid chiefly when there is a greater chance of larger broods being raised, the average clutch will probably not be that from which on average, most young are raised per brood." This is a possibility in the Red-billed Gull, since three chick broods in some years are more productive than smaller clutches, and this corresponds to the time when the greatest number of three egg clutches are laid.

Production and survival of young

The number of eggs producing fledged young depends on the date of laying, the position of the nest on the colony, the type of colony and the clutch size. Generally, the gulls that lay the earliest or at the peak laying period produce the greatest proportion fledged. The gulls which nest late in the season tend to nest on the periphery of the colonies or on the edges of groups of breeding gulls. These nests tend to be the most susceptible to predation and swamping. Similarly, newly established colonies have less breeding success than old colonies mainly because they are poor nesting habitats. Some colonies and study areas show a relationship between the number of gulls laying at a given period and the subsequent breeding success. Patterson (1965) and Kruuk (1964) believe that synchronised laying reduces predation. In the study areas and colonies which show a correlation between percentage breeding and subsequent breeding success the value of the coefficient is low, indicating that only a small proportion of breeding success is accounted for by this phenomenon. The breeding success is more closely correlated with the date of laying. Many young from late broods die in the nest and many which are successfully fledged do not survive for long.

There was a statistical difference in the percent hatching or percent fledged in different aged females but there was no marked trend for hatching or fledging success to increase with the age of the female. However, there was a progressive increase in the number of chicks fledged per pair up to the fifth year due to older gulls laying larger clutches and therefore raising more chicks per pair. Similarly, there was no difference in breeding success between females retaining or changing mates. The samples were small and the subject requires further investigation, since Coulson (1966) for the Kittiwake Gull *Rissa tridactyla* found that females retaining mates fledged significantly more chicks than females changing mates. Slightly more eggs are hatched from two and three egg clutches than from single egg clutches. The main cause of the difference is that greater numbers of single egg clutches are lost by predation. Brown (1967) considers that this is because single egg clutches present lower incubation stimuli to the parents, resulting in diminished attentiveness which contributes to greater egg predation by neighbouring gulls. Brown has not checked to see whether the single egg clutches were incubated by young gulls. It may be that the lower incubation drive is associated with younger gulls. The predation rate on nests of Red-billed Gulls is higher in younger gulls, especially in nests of young males. There is another possibility as well, since younger gulls tend to nest on the periphery of nesting colonies which are more susceptible to predation.

The post-fledging survival depends mainly on the date of hatching and the age of the parent. There was no difference found in the proportions surviving from broods of different sizes. The post-fledging survival of different sized broods in relation to date of hatching is confusing with no consistent yearly pattern. Perrins (1965) believes this may be because conditions for rearing young vary so much each season.

Chicks of young parents (2 - 3 years) had a statistically lower post-fledging survival than chicks of gulls over three years. It is likely that chicks from young gulls are not as well fed as chicks from older parents, and therefore have less fat which is a disadvantage when the chicks become independent. There is evidence that the later the bird breeds the less likely it is to produce surviving young, irrespective of the age of the parent. In these cases it appears that late breeders are unable to provide sufficient food to the chicks for deposition of internal fat reserves.

Competition for the available food in the pre-breeding period

The return to Kaikoura of large numbers of gulls in July places a severe demand on the food resources of the environs of Kaikoura. Most arrive before the plankton abundance has increased. The peak in euphausiid numbers does not occur until November - December. An indication of the food shortage is given by the marked decrease in mean body weight found in mid September (Figure 7 and Table 16). The variability of body weights of gulls showed that not all of the individuals in the population were affected. The most severely affected were gulls in the younger age classes, but even within these the variability of weights was large. This competition for food could account for the increase in adult mortality in spring. In several other bird species it has been observed that some individuals compete more successfully for food than others; for example tropical oceanic sea birds (Ashmole, 1963); the Australian Magpie *Gymnorhina tibicen* (Carrick, 1963); the Silver Gull *Larus novaehollandiae* (Carrick & Murray, 1964); and the Woodpigeon *Columba palumbus* (Murton, Isaacson & Westwood, 1966). Carrick & Murray (1964) consider that social status confers feeding rights, and the hostility shown by conspecific individuals for the necessities of life could well be the means whereby aspiring newcomers are denied adequate feeding rights. This point has also been stressed by Wynne-Edwards (1962).

In an intensive feeding study of Woodpigeons, Murton, Isaacson & Westwood (1966) found that a feeding flock maintained a relatively stable structure, and in general each bird remained in a constant position relative to others in a flock. They added that a true social hierarchy might imply that pigeons were able to recognise each other as individuals, but this need not be so since the same results could be achieved if the pigeon adopted a position in the flocks where it felt most at ease. In the Woodpigeon, individuals at the front of the flock obtained considerably less food than those in the centre or rear. Hence, some pigeons were continually denied food. There was no obvious displacement by fighting as has been observed among Rooks *Corvus frugilegus* by Lockie (1956), but rather supplanting attacks that were very subtle, and Murton, Isaacson & Westwood (1966) could not decide whether movement arose because a bird first moved towards another or whether a movement away created a vacant place.

In many photographs, (e.g. Plate 1), large numbers of gulls can be seen sitting on the water some distance from the swarm. Unfortunately, it is not known whether gulls have already obtained sufficient food, and so moved away from the flock, or whether they are birds unable to compete with other gulls. Observations of flocks feeding on intertidal regions and on land have shown that disputes are common. When food is in short supply, a wide area is temporarily defended by overt posture, mainly the forward and oblique postures (see Moynihan, 1955; Tasker, 1970). When food is particularly abundant, the density of birds increases and displays are less frequent, but there are continual "growling" calls given in the feeding posture, which effectively maintain individual distance. These observations on land are probably relevant to flock feeding at sea. While more evidence would be desirable, it is possible that the structure of feeding flocks is similar to that of pigeon flocks seen by Murton, Isaacson & Westwood. It is not known which positions within the flocks are the most successful but the frontal positions, where density is highest, seem likeliest.

Population increase

During this century Red-billed Gull numbers have increased spectacularly. Oliver (1955) has suggested that the most important factor in the gull population increase has been the utilization of the food supply made available by the establishment of freezing works, whaling stations, shipping centres and garbage dumps. Although this food is not utilized to any extent in the breeding season, large populations are supported by it in the autumn and winter. The importance of this food source is that it is an alternative food supply which is able to support more birds. The age structures of gulls feeding at the Christchurch Heathcote-Avon Estuary and in the Central Christchurch area differ. Relatively more juveniles are found at Central Christchurch, where the gulls depend on food given by the public, than are found at the estuary where the food supply is largely "natural". It seems, therefore, that the additional food supply allows unsuccessful and inexperienced birds to survive which may not if they remained at natural feeding grounds. In addition, the increase in food supply may allow birds to arrive at the breeding grounds in better breeding condition.

Another factor which could conceivably increase the population is an improvement in the availability of food at the breeding grounds. Since the population of Baleen Whales has been reduced to about one tenth of their original size, it might be expected that there is an excess production of euphausiids, previously harvested by the whales (Mauchline & Fisher, 1969). This would mean that competition for available plankton would be reduced. If individual gulls are able to obtain more food they may lay large clutches and raise more chicks per nest than previously. Many plankton feeders have increased in status in the last few years, for example, the Crab-eater Seals (Mauchline & Fisher, 1969) and the Fulmar *Fulmar glacialis* (Fisher, 1952). The increase in the Gannet *Sula bassana* populations could have benefited indirectly through an increased plankton production. All authors commenting on the population increase in sea bird populations have overlooked this as a possible factor.

10. SUMMARY

1. This thesis describes the results of a study of a Red-billed Gull _Larus novaehollandiae scopulinus_ population containing many birds of known age.

2. The Kaikoura gull population is increasing. Between 1964 and 1968 three new colonies were established.

3. Adults were sexed by a combination of bill measurements, depth at gonys and bill length. With a 99% confidence interval a discriminant function analysis gave the probability of misclassification of the sex of less than 9.1%.

4. Band loss was greatest with butt to butt bands and least with lock bands. Females suffered greater band losses than did males.

5. The sex ratio of banded gulls captured in the pre-breeding did not differ significantly from a 50:50 ratio. In the breeding period significantly more banded males than females were captured. Possible reasons for this are discussed.

6. Winter recoveries favoured males. The possible causes are considered.

7. The hatching period coincides with the peak abundance of adult euphausiids, the main diet of adult and nestling gulls. Changes in body weight in the pre-breeding period suggest that food shortage is affecting some of the gulls, particularly young ones.

8. The gulls return to the colonies in late June having been away since January. Occupation of nest sites begins in late August or early September. In the pre-breeding period females spend over twice as long at the nest territory than males. The preferred nest sites are central and elevated areas. Males, but not females, tend to breed at their natal colony.

9. The age at first breeding is variable; they are capable of breeding at two years, but the majority breed first at three, four and five years and some even later. Males tend to breed at a younger age than females.

10. Gulls tend to have partners of similar age. About 64% had mates with an age difference of no more than one year.

11. There is a marked tendency for gulls to retain the pair bond of the previous season. This is more marked in older gulls. Many of the new mates of gulls changing partners are inexperienced.

12. In the seasons from 1965-66 to 1968-69, the first egg was laid by 11 October. In each season, peak laying occurred at the same time in most study areas, and the mean and median laying dates of the same study area were remarkably consistent from year to year. Greater synchrony of laying occurs on elevated sites.

13. The incubation period varied between 21 and 27 days. Males and females spend a similar amount of time in the nest territory during incubation.

14. The normal clutch is two eggs. The clutch size of individual gulls did not differ significantly between 1967-68 and 1968-69.

15. There was no significant difference in hatching or fledging success between 1967-68 and 1968-69, but the atypical nesting colony studied in 1964-65 had a lower breeding success than the others. The most common cause of egg mortality was predation by Red-billed Gulls and Stoats <u>Mustela erminea</u>. Swamping of nests and predation caused loss of the entire clutch.

16. The date of egg laying affected clutch size, fledging success and post-fledging survival. Evidence suggests that laying at the peak period reduces predation.

17. The age of the female influences the date of laying,

clutch size, and post-fledging survival of chicks. The hatching and fledging success of different aged birds was statistically different but there was no marked tendency for increasing hatching or fledging success with an increase in age.

18. The significance of "courtship feeding" of the female by the male is discussed. The age of the male relative to the age of the female influenced the date of laying, clutch size and post-fledging survival.

19. Females which retain the pair bond from the previous season bred earlier in the season and laid more and larger eggs than females changing mates but no difference was found in the breeding success.

20. Single egg clutches had a smaller percentage hatch than larger clutches. The brood size of three was the largest the adults could normally feed. No difference was found in the post-fledging survival of different brood sizes.

21. The age structures of new and old colonies are examined. The breeding success is lower at new colonies; predation and swamping are the main mortality agents.

22. Replacement laying takes 7 - 33 days. The mean clutch size of replacement clutches was lower than original clutches but only 28% laid smaller clutches than the original. The breeding success of replacement clutches is higher than that of original clutches.

23. Deferred maturity and its significance is discussed.

24. In this population emigration exceeds immigration.

25. The causes of mortality are discussed. Seasonal mortality patterns differ in different age gulls. Mortality is low during the winter for gulls of all ages. Mortality is highest immediately upon fledging and decreases as the year progresses. One year old gulls have a peak mortality period in January and a secondary peak in May, while adult

gulls have a peak from early spring to late summer. The causes of the patterns are discussed.

26. Recovery data shows higher survival of males but other evidence suggests that female survival is greater.

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APPENDIX ONE

Locality and number of Red-billed Gulls banded as chicks in New Zealand and outlying islands from 1943 to 31 March 1970 (C.J.R. Robertson, pers. comm.)

Locality	No. banded
New Zealand	
Brothers Island	531
Castlepoint	43
Crusoe Island	58
Cuvier Island	17
Haast Rv. Mth	91
Kaikoura	25,044
Kapiti Island	1,266
Karitane	2
Kawakawa	45
Koi Island	4
Kuaotuna Beach	287
Lake Grassmere	2,429
Lake Rotorua	112
Mataikona	21
Moturoa Island	14
Nawhi Point	101
Nelson	2,680
New Plymouth	572
Okarito Rv. Mth	4
Onekapua Point	20
Picton	50
Porongahau	29
Pourakino River	12
Renewahine Point	3
Stephens Island	173
Three Kings Islands	50
Tiri Tiri Island	106
Waiwakaiho Rv. Mth	8
Whale Island	5
White Island	13
White Rock	38
Total for New Zealand	33,828
Outlying islands	
Auckland Islands	34
Campbell Islands	80
Chatham Islands	18
Snares Island	29
Total for outlying islands	161

APPENDIX TWO

Proportion of bands illegible

Band Type: A

	Number of years band worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. bands examined	2	0	0	1	3	1	2	1	0	9	9
Percent illegible	0%	-	-	0%	0%	0%	0%	0%	-	0%	0%

Band Type: B

	Number of years band worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. bands examined	3	0	1	1	0	2	0	0	0	4	
Percent illegible	0%	-	0%	0%	-	0%	-	-	-	0%	

Band Type: C

	Number of years band worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. bands examined	24	16	8	4	17	50	100	1	0	13	
Percent illegible	0%	0%	0%	0%	0%	0%	0%	0%	-	0%	

(APPENDIX TWO continued)

Band Type: D

	Number of years band worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. bands examined	43	33	13	9	4	0	0	92	98	441	
Percent illegible	0%	0%	0%	0%	0%	-	-	2%	4%	13%	

Band Type: E

	Number of years band worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. bands examined	4	4	19	92	69	25					
Percent illegible	0%	0%	0%	0%	0%	0%					

APPENDIX THREE

Differential band loss from male and female Red-billed Gulls

Band Type: A

(a) Females

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. females considered	-	-	-	-	2	5	4	4	3	8
No. females that lost a band					0	1	0	1	2	6
Percentage lost					0.0	20.0	0.0	25.0	66.7	75.0
Cumulative percent lost					0.0	20.0	20.0	40.0	80.0	95.0

(b) Males

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. males considered	-	-	-	-	1	3	4	5	9	9
No. males that lost a band					0	0	0	0	1	1
Percentage lost					0.0	0.0	0.0	0.0	11.1	33.3
Cumulative percent lost					0.0	0.0	0.0	0.0	11.1	40.7

(APPENDIX THREE continued)

Band Type: C

(a) Females

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. females considered	1	1	1	3	10	30	6	4	6	2
No. females that lost a band	0	0	0	0	1	2	1	1	2	1
Percentage lost					10.0	6.7	16.7	25.0	33.3	50.0
Cumulative percent lost					10.0	16.0	30.0	47.5	61.6	80.8

(b) Males

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. males considered	2	2	2	5	25	50	10	3	10	2
No. males that lost a band	0	0	0	0	0	1	1	0	2	1
Percentage lost	0.0	0.0	0.0	0.0	0.0	2.0	10.0	0.0	20.0	50.0
Cumulative percent lost	0.0	0.0	0.0	0.0	0.0	2.0	11.8	11.8	29.4	64.7

(APPENDIX THREE continued)

Band Type: E

(a) Females

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. females considered	147	23	17	15	16	2				
No. females that lost a band	0	0	0	0	0	0				
Percentage lost	0.0	0.0	0.0	0.0	0.0	0.0				
Cumulative percent lost	0.0	0.0	0.0	0.0	0.0	0.0				

(b) Males

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. males considered	272	48	64	50	28	2	1			
No. males that lost a band	0	0	0	0	0	0	0			
Percentage lost	0.0	0.0	0.0	0.0	0.0	0.0	0.0			
Cumulative percent lost	0.0	0.0	0.0	0.0	0.0	0.0	0.0			

(APPENDIX THREE continued)

Band Type: D

(a) Females

	Number of years the band has been worn									
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10
No. females considered	-	-	-	-	5	8	35	43	26	3
No. females that lost a band					0	0	1	1	1	0
Percentage lost					0.0	0.0	2.9	2.3	3.8	0.0
Cumulative percent lost					0.0	0.0	2.9	4.5	8.1	8.1

(b) Males

	Number of years the band has been worn										
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11
No. males considered	-	-	-	4	10	16	49	67	40	7	2
No. males that lost a band				0	0	0	0	1	0	0	0
Percentage lost				0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0
Cumulative percent lost				0.0	0.0	0.0	0.0	1.5	1.5	1.5	1.5

APPENDIX FOUR

(a) Seasonal variation of clutch size 1965-66

Date	No. clutches	Clutch size 1	2	3	4	Mean clutch	S.D.	Percent composition 1	2	3	4
17-23 Oct.	125	16	88	20	1	2.05	0.57	13%	70%	16%	1%
24-30 Oct.	90	9	63	17	1	2.11	0.57	10%	70%	19%	1%
31- 6 Nov.	112	10	90	12		2.02	0.44	9%	80%	11%	
7-13 Nov.	92	13	72	7		1.93	0.46	14%	78%	8%	
14-20 Nov.	86	12	68	6		1.93	0.45	14%	79%	7%	
21-27 Nov.	87	15	62	9	1	1.95	0.57	18%	71%	10%	1%
28- 4 Dec.	44	10	34			1.77	0.42	23%	77%		
5-11 Dec.	54	13	38		3	1.87	0.67	24%	70%		6%
12-18 Dec.	27	12	15			1.56	0.51	44%	56%		
19-25 Dec.	9	6	3			1.33	0.50	67%	33%		

(APPENDIX FOUR continued)

(b) Seasonal variation of clutch size 1967-68

Date	No. clutches	Clutch size 1	2	3	4	Mean clutch	S.D.	Percent composition 1	2	3	4
3- 9 Oct.	22	2	17	3		2.05	0.49	9%	77%	14%	
10-16 Oct.	153	12	105	36		2.16	0.54	8%	69%	23%	
17-23 Oct.	146	15	108	23		2.05	0.51	10%	74%	16%	
24-30 Oct.	295	17	253	24	1	2.03	0.39	6%	85%	8%	1%
31- 6 Nov.	132	11	115	6		1.96	0.36	8%	87%	5%	
7-13 Nov.	88	17	68	3		1.84	0.45	19%	77%	4%	
14-20 Nov.	53	7	40	6		1.98	0.50	13%	76%	11%	
21-27 Nov.	47	16	31			1.66	0.48	34%	66%		
28- 4 Dec.	38	11	27			1.71	0.46	29%	71%		
5-11 Dec.	26	9	17			1.65	0.49	35%	65%		
12-18 Dec.	8	3	5			1.63	0.52	38%	62%		
19-25 Dec.	12	4	8			1.67	0.49	33%	67%		

(APPENDIX FOUR continued)

(c) Seasonal variation of clutch size 1968-69

		Clutch size							Percent composition				
Date	No. clutches	1	2	3	4	5	Mean clutch	S.D.	1	2	3	4	5
3- 9 Oct.	3		2	1			2.33	0.58		67%	33%		
10-16 Oct.	79	3	62	14			2.14	0.45	4%	78%	18%		
17-23 Oct.	275	17	231	27			2.04	0.40	6%	84%	10%		
24-30 Oct.	143	15	109	18		1	2.04	0.47	11%	76%	13%		1%
31- 6 Nov.	156	14	134	8			1.96	0.41	9%	85%	5%		
7-13 Nov.	62	9	50	3			1.90	0.43	14%	81%	5%		
14-20 Nov.	66	9	54	3			1.91	0.42	14%	82%	4%		
21-27 Nov.	32	7	23	2			1.84	0.52	22%	72%	6%		
28- 4 Dec.	45	11	33	1			1.78	0.47	25%	73%	2%		
5-11 Dec.	23	5	18				1.78	0.42	22%	78%			
12-18 Dec.	13	2	11				1.85	0.38	15%	85%			
19-25 Dec.	12	8	4				1.33	0.49	67%	33%			
26- 1 Jan.	5	2	3				1.60	0.55	40%	60%			

APPENDIX FIVE

Correlation between the number of gulls laying and the subsequent breeding success

Colony: Lighthouse
Area A (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	178 gulls	0.5%	12.9%	17.4%	14.6%	20.8%	13.5%	3.4%	6.2%	7.9%	1.7%		1.1%
Breeding success	No. eggs laid	2	18	39	43	33	28	7	20	18	2		2
	% fledged	100%	44.4%	79.5%	69.8%	39.4%	53.6%	0%	55.0%	22.2%	50.0%		100%
	Kendal rank correlation	τ = +0.15, p = > 0.10											

Colony: Lighthouse
Area B (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	100 gulls	10.0%	18.0%	15.0%	26.0%	9.0%	5.0%	5.0%	4.0%	3.0%	5.0%		
Breeding success	No. eggs laid	19	38	23	45	12	10	7	7	5	6		
	% fledged	68.4%	52.6%	82.6%	64.4%	91.7%	50.0%	57.1%	71.4%	0.0%	0.0%		
	Kendal rank correlation	τ = +0.24, p = > 0.10											

Colony: Iceplant
Area A (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	52 gulls			7.6%	32.7%	17.3%	17.3%	7.6%	3.8%	5.8%	3.8%	1.9%	1.9%
Breeding success	No. eggs laid			6	16	9	11	10	2	4	2		
	% fledged			83.3%	68.8%	100%	72.7%	50.0%	50.0%	100%	0.0%		
	Kendal rank correlation	τ = +0.29, p = > 0.10											

Colony: Iceplant
Area B (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	65 gulls			26.0%	41.5%	12.3%	3.1%	1.5%	12.3%				
Breeding success	No. eggs laid			28	24	6	4		9				
	% fledged			64.3%	75.0%	50.0%	25.0%		66.7%				
	Kendal rank correlation	τ = +0.6, p=0.10											

(APPENDIX FIVE continued)

Colony: Rhinohorns
Area A (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	146 gulls	0.7%	7.5%	6.8%	34.9%	14.4%	17.8%	7.5%	6.8%	3.4%			
Breeding success	No. eggs laid	2	13	8	73	34	29	11	11	6			
	% fledged	0.0%	69.2%	75.0%	71.2%	47.1%	55.2%	27.3%	81.8%	16.7%			
	Kendal rank correlation τ = -0.15, p = 0.10												

Colony: Rhinohorns
Area B (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	45 gulls		8.9%	13.3%	51.1%	11.1%	2.2%	4.4%	2.2%	6.7%			
Breeding success	No. eggs laid		5	11	34	9	2		1	3			
	% fledged		20.0%	43.5%	58.8%	55.6%	0.0%		0.0%	33.3%			
	Kendal rank correlation τ = +0.62, p = 0.050												

Colony: Rhinohorns
Area C (1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	101 gulls	9.9%	24.8%	16.8%	36.6%		8.9%	3.0%					
Breeding success	No. eggs laid	15	45	17	62		13	4					
	% fledged	53.3%	64.4%	82.4%	62.9%		92.3%	75.0%					
	Kendal rank correlation τ = -0.40, p = > 0.10												

Colony: Frank's
(1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	114 gulls			7.9%	39.4%	10.5%	3.5%	8.8%	1.8%	4.4%	13.2%	6.1%	4.4%
Breeding success	No. eggs laid			11	85	24	8	21		6	28	11	9
	% fledged			0.0%	62.4%	50.1%	50.0%	71.4%		50.0%	0.0%	0.0%	0.0%
	Kendal rank correlation τ = +0.2, p = > 0.10												

(APPENDIX FIVE continued)

Colony: Avoca
(1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	120 gulls		9.2%	23.3%	35.0%	14.2%	5.8%	2.5%	5.8%	3.3%			0.8%
Breeding success	No. eggs laid		25	46	59	33	8	5	10	7			2
	% fledged		64.0%	37.0%	37.3%	3.3%	0.0%	0.0%	0.0%	0.0%			0.0%
	Kendal rank correlation τ = +0.58, p = 0.025												

Colony: Lagoon
(1967-68)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	61 gulls		8.2%	24.6%	14.8%	23.0%	3.3%			1.6%	16.4%	8.2%	
Breeding success	No. eggs laid		11	16	20	21	4			2	12	5	
	% fledged		0.0%	0.0%	0.0%	0.0%	0.0%			0.0%	0.0%	0.0%	

Colony: Lighthouse
Area A (1968-69)

		Seven day periods after commencement of laying												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Distribution of egg laying	159 gulls		8.2%	27.7%	10.1%	13.2%	5.0%	11.3%	3.8%	6.3%	6.9%	3.8%	3.1%	6.3%
Breeding success	No. eggs laid		21	79	26	21	9	26	8	13	12	4	2	1
	% fledged		42.9%	63.3%	34.6%	28.6%	44.5%	19.2%	37.5%	15.4%	58.3%	100%	0.0%	100%
	Kendal rank correlation τ = -0.015, p = > 0.10													

Colony: Lighthouse
Area B (1968-69)

		Seven day periods after commencement of laying												
		1	2	3	4	5	6	7	8	8	10	11	12	13
Distribution of egg laying	86 gulls		5.8%	18.6%	16.3%	12.8%	11.6%	14.0%	3.5%	10.5%	1.2%	1.2%	4.7%	
Breeding success	No. eggs laid		9	28	29	25		22	4	9		2	7	
	% fledged		0.0%	35.7%	62.1%	36.0%		40.9%	50.0%	56.3%		0.0%	0.0%	
	Kendal rank correlation τ = +0.22, p = > 0.10													

(APPENDIX FIVE continued)

Colony: Iceplant
Area A (1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	105 gulls		4.8%	23.8%	19.0%	26.7%	6.7%	8.6%	2.9%	3.8%		1.9%	1.9%
Breeding success	No. eggs laid		8	47	33	53	12	16	5	5			1
	% fledged		75.0%	70.2%	72.7%	62.2%	50.0%	37.5%	40.0%	0.0%			0.0%
	Kendal rank correlation τ = +0.42, p = 0.10 - 0.05												

Colony: Iceplant
Area B (1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	55 gulls		14.5%	34.5%	21.8%	10.9%		7.3%	5.5%	1.8%			3.6%
Breeding success	No. eggs laid		16	41	16	9		4				4	
	% fledged		68.8%	75.6%	68.8%	77.8%		50.0%				75.0%	
	Kendal rank correlation τ = +0.07, p = > 0.10												

Colony: Rhinohorns
Area A (1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	113 gulls		15.0%	31.9%	9.7%	16.8%	11.5%	3.5%	2.7%	1.8%	4.4%	1.8%	0.9%
Breeding success	No. eggs laid		35	62	20	30	16	4	4	2	6	4	1
	% fledged		54.3%	62.9%	50.0%	56.7%	37.5%	25.0%	0.0%	0.0%	20.0%	25.0%	0.0%
	Kendal rank correlation τ = +0.82, p = < 0.005												

Colony: Rhinohorns
Area B (1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	77 gulls		10.4%	33.8%	14.3%	24.7%	5.2%	5.2%		1.3%	6.5%		
Breeding success	No. eggs laid		16	41	16	9		4			4		
	% fledged		68.8%	75.6%	68.8%	77.8%		50.0%			75.0%		
	Kendal rank correlation τ = +0.13, p = 0.10												

(APPENDIX FIVE continued)

Colony: Rhinohorns
Area C (1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	95 gulls	2.1%	24.2%	34.7%	21.2%	7.4%	3.2%			7.4%			
Breeding success	No. eggs laid	4	50	66	28	10	6			5			
	% fledged	100%	76.0%	65.2%	60.7%	60.0%	100%			40.0%			
	Kendal rank correlation $\tau = -0.14, p = 0.10$												

Colony: Frank's
(1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	100 gulls		5.0%	30.0%	18.0%	12.0%	8.0%	6.0%	6.0%	12.0%	3.0%		
Breeding success	No. eggs laid		7	64	35	24	12	5	12	22	6		
	% fledged		57.1%	59.4%	37.1%	41.7%	33.3%	20.0%	0.0%	13.6%	0.0%		
	Kendal rank correlation $\tau = +0.44$, $p = 0.05$												

Colony: Lagoon
(1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	95 gulls	4.2%	26.3%	16.8%	8.4%	26.3%	6.3%	11.6%					
Breeding success	No. eggs laid	4	43	27	16	47	10	17					
	% fledged	0.0%	44.2%	70.4%	0.0%	25.0%	0.0%	0.0%					
	Kendal rank correlation $\tau = +0.43, p = 0.10$												

Colony: Avoca
(1968-69)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	20 gulls		60.0%	40.0%									
Breeding success	No. eggs laid		19	10									
	% fledged		0.0%	0.0%									

(APPENDIX FIVE continued)

Colony: Sugarloaf
(1965-66)

		Seven day periods after commencement of laying											
		1	2	3	4	5	6	7	8	9	10	11	12
Distribution of egg laying	294 gulls	5.4%	16.3%	12.2%	19.7%	13.6%	8.8%	17.0%	3.7%	2.4%	0.3%	0.3%	
Breeding success	No. eggs laid	36	98	70	122	79	50	75	22	12	2	1	
	% fledged	33.3%	36.7%	24.3%	39.3%	15.2%	0.0%	6.0%	4.4%	0.0%	0.0%	0.0%	
	Kendal rank correlation τ = +0.65, p = <0.005												